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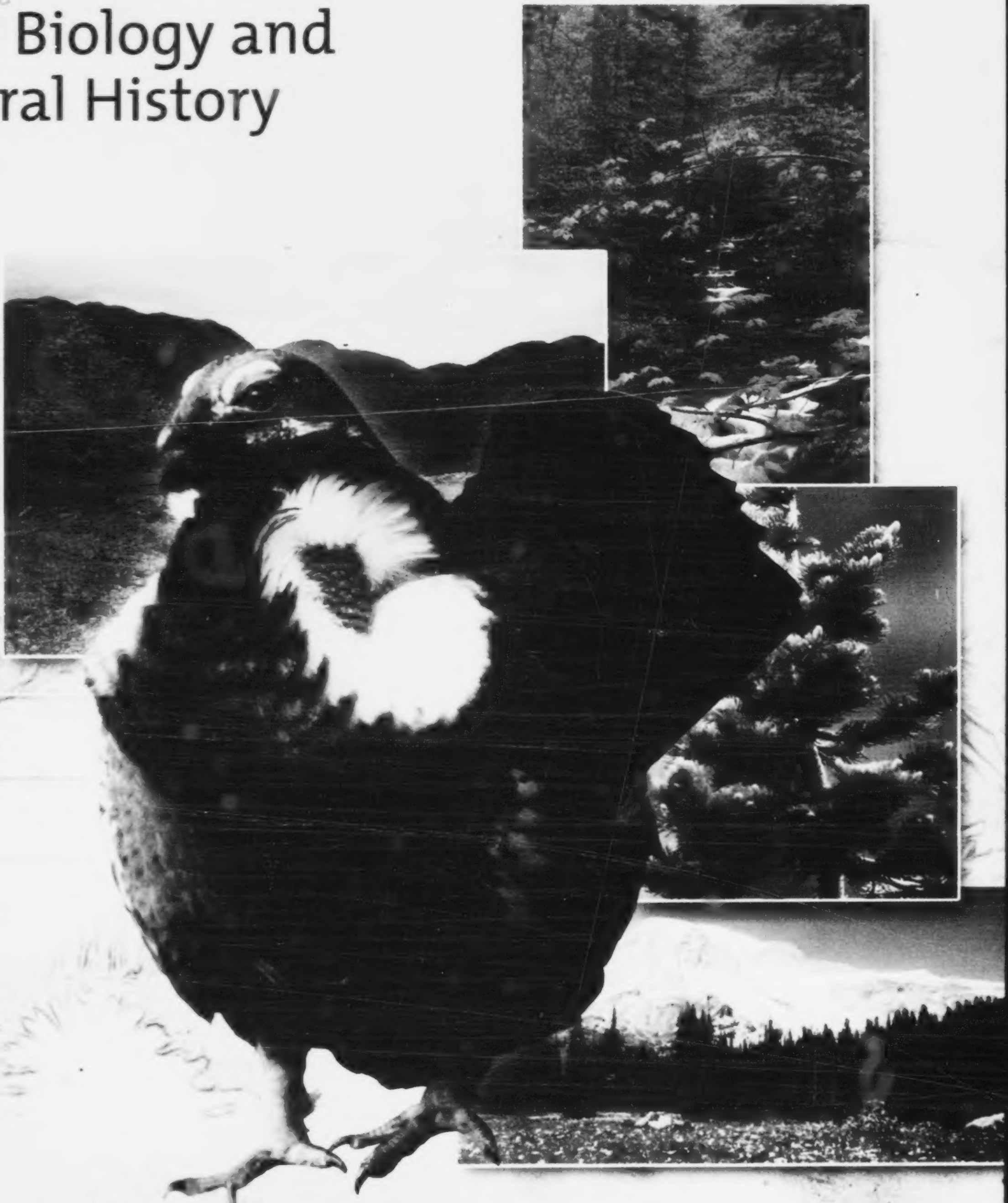
BLUE GROUSE

Their Biology and Natural History



Fred C. Zwickel
James F. Bendell

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NRC Monograph Publishing Program

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Blue Grouse

Their Biology and Natural History

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Dedicated to the many students and other colleagues who contributed enthusiasm, time, energy, ideas, and so much more to our studies

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Preface

Indeed, hypothesis testing in the absence of the necessary background provided by natural-history studies is likely to be a sterile and meaningless activity.

JA Wiens (1989)

Prior to 1900, little was published about blue grouse other than short notes concerning their natural history, taxonomy, and distribution, or descriptions of them in general bird books. A number of more directed papers on various aspects of their natural history appeared in the next 40 years, but no longer term work. The first focussed ecological studies were begun by Leonard Wing and his colleagues in Washington State in 1940, followed closely by the work of C David Fowle in British Columbia. We first began to work with this grouse in 1950 (JF Bendell) and 1953 (FC Zwickel) and were involved in more or less continuous field or aviary studies with it until 1986. Beginning in the 1940s and 1950s, many short and longer term studies were completed by others in various parts of its range. In the early 1980s, after some three decades of working with this bird, we began to consider the preparation of a monograph. This book is a contribution toward that monograph.

Our interests have been primarily focussed on population biology and behaviour, but we also collected large amounts of natural history, and other data. Although our eventual aim is to explain how the abundance and distribution of blue grouse might be determined, we make no excuses for devoting much attention to their biology and natural history. In our view, a thorough knowledge of our study animal is fundamental to understanding its populations. For example, census is an important technique for understanding abundance and distribution and cannot be accurate without knowing who is where at what time. Many elements of biology will be involved in processes determining population levels, and general theory depends on how solid are the facts on which it is built.

Owing to our decades-long work and the many other studies of blue grouse in recent decades, this first monograph describes many aspects of the biology and natural history of blue grouse. It is divided into five parts and 20 chapters. Three chapters briefly introduce blue grouse and the Tetraoninae; some of the approaches used in our studies; and the principal studies and investigators on whose work we have drawn. Four chapters provide further background material about the species. One reviews past and current taxonomy, the continental distribution of blue grouse and its extant subspecies, local extirpations, island populations, and introductions into unoccupied range. The next is devoted to evolution. The bird's fossil history is reviewed, and an argument is made for its evolution from a prairie grouse-like ancestor. We propose a northward radiation of the species from a southern point of origin. Aboriginal uses and historical records of early explorers and naturalists are considered in the third chapter of this section. Physical attributes of the environments occupied by blue grouse—the montane terrain, climate, weather, and plant communities—are examined in the fourth chapter. Next, seven chapters are devoted to the physical and functional attributes of the species. Topics include the following: the integument, morphology, reproduction, growth and development, food habits and nutrition, energetics, and genetics. Variations among sex and age classes are identified, and comparisons among populations and subspecies are made. Behaviour is the focus of the next three chapters. The first describes and discusses individual and collective actions and reactions of this grouse. Items such as postures, flight, vocalizations, sociality, courtship displays, aggression, defence of nests, brooding of young, and flocking are examined. Two important consequences of behaviour, "use of habitat" and "movements and use of space", are explored in the following two chapters. The first examines what aspects of the habitat may be selected for, or avoided, and the latter concerns migration, dispersal, and home ranges. Three chapters constitute the last section of this book, all of which relate to populations. The first documents the principal parameters of populations that contribute to their dynamics—density, sex and age structure, survival, and production. Next, the seasonal pattern of predation on males, females, and juveniles is considered. Sexes and ages of birds killed and kinds of predators are identified. The special circumstance of predation on nests is discussed. Lastly, the reported diseases and parasites of blue grouse are reviewed. A future volume will emphasize the population ecology of blue grouse and its relation to population theory. It will lean heavily on information in this publication.

In writing about this species, we feel obliged to be as comprehensive as possible. Material here is principally documentary, with implications of some of the data unexplored. Unexplored data are offered because an unrelated fact to us may provide a piece of a different puzzle to another. We estimate that this book contains at least 50% new material, largely from our own work. The remainder reviews, consolidates, and compares results of other studies with ours.

Most of the writing of this manuscript was done by the senior author FC Zwickel. JF Bendell contributed to planning and organization of the book, provided information, concepts, photos, and critical editing.

We present this work to share what we think is of value and, to return in some way, the support we have received. Perhaps this brief background will place the contents in context and warn of some of our biases.

Abstract/Résumé

This monograph is about blue grouse (*Dendragapus obscurus*). Designed as a reference work, it documents and reviews much of what is known about the biology and natural history of this bird. It is based primarily on our published and unpublished long-term studies in British Columbia and elsewhere, and on the studies of others in various parts of the bird's range. Part 1 is principally introductory, describing some of our approaches and introducing the principal studies and study areas on which the book is based. Part 2 provides background to the bird, e.g., its taxonomy, evolution, and the environment in which it lives. Physical attributes, e.g., its morphology, reproduction, and food habits are examined in Part 3. Part 4 is devoted to individual and collective behaviours, a field of study that we feel has important implications to populations. Lastly, Part 5 documents the principal population parameters of this grouse and identifies some of what is known about its predators and diseases, agents potentially important to prey populations.

La présente monographie porte sur le tétras sombre (*Dendragapus obscurus*). Elle se veut un ouvrage de référence qui documente et passe en revue les principaux faits connus de l'histoire biologique et naturelle de cet oiseau. Elle repose essentiellement sur nos études de longue date, publiées ou non, réalisées en Colombie-Britannique et ailleurs ainsi que sur les études d'autres auteurs dans les divers secteurs de l'aire de répartition de l'oiseau. La partie 1 constitue une introduction, où sont présentés certaines des démarches empruntées dans nos études de même que les principaux travaux et secteurs de recherche dont nous nous sommes inspirés. La partie 2 propose des renseignements généraux sur l'espèce, p. ex. sa taxonomie, son évolution et son environnement. Les attributs physiques de l'espèce, p. ex. sa morphologie, sa reproduction et ses habitudes alimentaires, sont examinés dans la partie 3. La partie 4 porte sur le comportement individuel et collectif de l'oiseau, aspect que nous estimons déterminant pour les populations. Enfin, la partie 5 se penche sur les principaux paramètres de la population de l'espèce et décline les faits sur les prédateurs et les maladies connus, agents susceptibles d'avoir une incidence non négligeable sur les populations d'espèces prédatrices.

Acknowledgments

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Over the years, we have had many research assistants in the field and (or) laboratory, most of whom were undergraduate students. Most took a strong interest in our work, and a few did special studies that contributed new insights about blue grouse, some of which are cited here. FA Gornall and AN Lance pioneered our holding of blue grouse for aviary study and contributed in other ways. DT McKinnon supervised field crews at Hardwicke Island in 1984, Duck Creek, NV, in 1985, and Skalkaho, MT, in 1986. MA Degner supervised field work at the May Ranch, CA, in 1984, and Hudson Bay Mountain, BC, in 1985. McKinnon, Degner, P Zuest, P McConnachie, and W Ebensberger, as research assistants, contributed to our research in many ways.

We visited and examined, at least cursorily, blue grouse populations in their natural habitats in all provincial, territorial, and state political jurisdictions where they occur except the Northwest Territories. All wildlife agency staff were extremely cooperative in providing help, information, permits, etc. In British Columbia, where most of our studies were done, J Bandy, D Eastman, J Hatter, D Robinson, E Taylor, and a number of Conservation Officers of the Wildlife Branch were especially supportive of our work. M Fenger, also of the BC Wildlife Branch, rented us his ski cabin at Hudson Bay Mountain in the summer of 1986. The late Bill McLellan allowed us to use his cabin at Lower Quinsam Lake for several years. D Dixon provided winter care for some of our dogs. JH Brigham, ER Brown, CF Martinsen, and JR Patterson, all of the Washington Department of Game, assisted in checking grouse shot by hunters, and in other ways, in some of our early studies in Washington State. United States Forest Service personnel provided us with maps, other information, permits, and, at Duck Creek, NV, summer accommodations. Studies at Lower and Middle Quinsam, BC, were on land controlled by Elk River Timber Co., and we worked there with their permission. Studies at Comox Burn were on land controlled by Crown Zellerbach, Canada, and their staff were most helpful—we especially appreciate the assistance of Ken Willis, Office Manager.

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MA Degner, SJ Hannon, DT McKinnon, and MG Sullivan assisted with data analyses and McKinnon, Sullivan, B Chernyk, and P Pearlstone provided advice on, and assistance with, some statistical procedures. MG Sullivan also contributed to some graphic presentations. M and H Trettin translated some Russian literature for us. JD Bland, DA Boag, CE Braun, NJ Braun, PW Elliott, SJ Hannon, JE Hines, DM Keppie, J Kristensen, JF Neiderleitner, MA Schroeder, and HL Zwickel read and commented on various aspects of the manuscript, helped eliminate errors, and contributed to our thinking. RM Zwickel assisted with preparation of the manuscript. We also acknowledge the many discussions, sometimes heated, we have had with other colleagues and from which we have benefited. Of special note are the late JR Adams, AT Bergerud, the late IO Buss, D Chitty, JB Falls, R Moss, A Watson, and the numerous students with whom we spent many months in field camps or the laboratory.

Drawings are by WJ Adams, RG Carveth, and ChW Gronau. Photographs are ours, unless noted otherwise, and those of others are credited in figure captions. We thank MA Degner, J Kristensen, RJ Long, W Lynch, SD McDonald, and R Zach for those we used.

We also acknowledge staff of the NRC Research Press who helped immeasurably with preparation of the manuscript for publication, including eliminating errors.

After more than three decades of more or less continuous study in the field and laboratory, and more than two of less intense field work, it is virtually impossible to acknowledge individually everyone who has encouraged or helped us, and every agency or other organization that has contributed in

some way to our work. We can only say, they number in the hundreds and express our appreciation to all.

Lastly, we thank our wives, Ruth and Yvonne, and children, who spent many summers in tents or rustic cabins, contributed to the operation and maintenance of our field camps, assisted in the field, laboratory, and office, and tolerated our eccentricities with grouse for more than 50 years.

Part 1
Introduction

CHAPTER 1

Blue Grouse Among the Tetraonines

There are grouse specialized to tundra habitats,
to open grasslands and to the various stages of forest succession.

I. Storch (2000)

Grouse, birds in the Subfamily Tetraoninae, constitute a small group of 19 recognized species in nine genera,[1] all confined to the northern hemisphere. They are considered an ancient group, well differentiated by the lower Miocene (Brodkorb 1964), the earliest epoch to which fossil grouse have been assigned (Johnsgard 1983). Two extant genera, *Falcipennis* and *Lagopus*, with two of its three species, are circumpolar. Other species occupy extensive ranges across much of northern Eurasia or North America, but some are very restricted.

The grouse occupy prairie grasslands and sagebrush (*Artemesia* spp.) desert, boreal and montane forest, and alpine and Arctic tundra (~28° to >80°N latitude). The species form a continuum of mating systems that range from monogamy and promiscuity on dispersed territories to promiscuity associated with communal display (so-called lek-displaying birds). The exact relationship between blue grouse (*Dendragapus obscurus*) and other species is still moot, for they share physical and behavioural traits with both "forest" and "prairie" species. Several attributes, including recent molecular evidence (Ellsworth et al. 1995, 1996; Gutierrez et al. 2000; Lucchini et al. 2001; Drovetski 2002, 2003), suggest a close relationship with prairie grouse in the genera *Tympanuchus* and *Centrocercus*.

Blue grouse have a relatively restricted geographic range and are endemic to mountainous regions of western North America, the Nearctic. Eight subspecies are often assigned to two clear groups, "interior" and "coastal", or "dusky" and "sooty", each with four subspecies. This bird still occurs throughout most of its historic range and occupies a diversity of breeding habitats, from sea level to alpine tundra. It is the seventh largest grouse, the third largest in North America (among 11 species) and is sexually dimorphic in plumage and body size. It can be found in low to very high densities, has a mostly diurnal activity pattern, and can be relatively unwary, easily captured, and conspicuous. These attributes make it a useful subject for research.

Like most north temperate birds, blue grouse have well-defined seasonal aspects in their annual cycle, e.g., distinct breeding and non-breeding periods. Most populations are locally migratory, spending the non-breeding season in coniferous forest and moving to more open forest, or other open plant communities, to breed. Males are polygynous and occupy and defend dispersed territories in the breeding season. Only females incubate eggs and care for the precocious, nidifugous young.

Endnote [Chapter 1]

1. North American species and genera as per AOU (1983) and AOU (2000), Eurasian as per Potapov (1985). Potapov retains the two recognized species of black grouse in the genus *Lyrurus*, but more recently they are usually considered congeneric with the two capercaillie in the genus *Tetrao*.

CHAPTER 2

Our Approach

> *Ecologists attempt to describe how organisms behave in nature and explain such fundamental questions as why certain organisms live in a particular place, what regulates their numbers and what differences occur within and between individuals and populations.*
>
> T Lewis and LR Taylor (1967)

We have used various approaches in our research, with study designs dependent on both overall and specific objectives. We have used descriptive, comparative, and experimental methods, each of which has strengths and weaknesses. As the principal investigators of intensive studies that spanned 1950–1986, we maintained as much continuity as possible over aspects of a long-term nature. At the same time, we and our colleagues, many of whom were students, conducted numerous subprojects, often designed to answer questions arising from earlier work. Here, we review some of the more general approaches and methods employed in our research and approaches used in this book.

2.1 Our own studies

2.1.1 Field studies

Our principal interest in population biology has required a strong emphasis on documenting and monitoring parameters of populations such as density, sex and age ratios, survival, and productivity. On our main study areas at Lower Quinsam, Middle Quinsam, Comox Burn (all on Vancouver Island, BC), and Hardwicke Island, BC, we attempted to capture and band as many grouse as possible. This involved near-daily searches by 1–4 persons, each usually accompanied by a trained pointing dog.[1] This work was concentrated on or adjacent to permanent study plots throughout the breeding season.

Unmarked birds were usually captured with "noosing poles" (Zwickel and Bendell 1967*a*). Captured birds were identified as to sex and age,[2] examined for primary moult, weighed, and lengths of one foot and (or) one wing were measured. Selected primaries were collected from one wing of each yearling and adult, and in many cases, selected rectrices were collected, so age (from primaries (Braun 1971)) and sex (from rectrices) could be confirmed in the laboratory. Beginning in 1972, one or two postjuvenal upper tail coverts were collected from juveniles ≥6 weeks of age for identification of sex (Nietfeld and Zwickel 1983). Yearlings, adults, and juveniles ≥4 weeks of age were marked with a numbered metal band and 1–4 colour bands. Beginning in 1972, many chicks too small to band were marked with numbered patagial wing tags. Subsidiary data such as behaviour and abnormalities were noted. Blood smears were made from most birds for study of blood parasites. Data for each bird were recorded on "band cards". Except where noted, these procedures were applied at all principal study areas.

Records were maintained of all sightings of marked and unmarked birds, with banded birds identified by their unique colour combinations. Each record included number of birds, their sexes and ages (if known), date, time of day, location, conspicuous vegetation at the site, weather, colour codes of marked birds, and pertinent behavioural data, all recorded on "sight cards". Although band and sight cards evolved over time, all of the above data were usually recorded at all areas.

We conducted a number of experimental removal studies aimed at identifying population processes. Results will be considered in some detail elsewhere, but since subsidiary data were also collected and are sometimes used in this book, some aspects of these studies should be noted.

Most birds taken from removal areas were killed.[3] Necropsies were performed immediately on most, or within 2–3 months after collection (carcasses had been frozen). Crop and gizzard contents of many were examined for items eaten, and many birds were examined for parasites. Selected external features and internal organs were examined and measured. Where appropriate,[4] these data, supplemented by those from birds collected for other reasons, were used to examine morphological parameters. Most skins and many other body parts are archived at the Royal Ontario and Royal British Columbia museums.

Development and refinement of radio-telemetry in the 1950s and 1960s opened new avenues of approach. Lance (1970) was first to use telemetry on blue grouse. We became significantly involved with the technique in the mid 1970s, after which it was used in several graduate programs. Although these birds were equipped with radios to answer specific questions, they also provided other information not readily available without this technology. For example, birds could usually be found at will for repeat observations of behaviour, and birds that died were more readily located. Transmitters did not seem to affect nesting success, clutch or brood sizes, movements, or survival (Hines and Zwickel 1985).

We also examined grouse shot by hunters. Wings, and in some cases tails, were collected from shot birds. These birds provided samples of sex, age, and body mass over larger areas than from our study areas. Examinations of shot birds at roadside "checking stations" also provided us with information on banded birds taken by hunters.

Until 1978, most of our studies were primarily of an intensive nature, on relatively restricted areas, and concentrated in coast forests in early stages of secondary succession. In the springs and summers of 1978 and 1979, we conducted a general survey of blue grouse in selected areas throughout their range (Bendell and Zwickel 1984). Main objectives were to compare populations and habitats that might be linked to abundance and distribution and to test the generality of results from our long-term work. We visited 43 areas from the southernmost (New Mexico, Arizona, California) to northernmost (Yukon Territory, Alaska) ranges of blue grouse. Owing to the extensive nature of this survey, we spent only 1–4 days in each area.

As a follow-up to the above survey, we examined four selected populations in more depth, each for one breeding season. Two southern populations were studied in year 1, two central populations in year 2 (one interior and one coastal population in year 1, two interior populations in year 2). Approaches and methods were, as far as possible, those used in our long-term work. Our principal objective was to more thoroughly test the generality of results from earlier work.

At most principal study areas, we type-mapped plant communities and surveyed vegetation within the different communities with plots or line transects. We maintained constant recording thermographs and totalizer rain gauges (Daubenmire 1947) on our main study areas throughout our field seasons.[5] In areas worked for >1 year, instruments were at the same locations each year. Being stationary, these "weather stations" do not reflect exact microhabitats used by individuals but provide data for comparisons among areas and (or) years.

2.1.2 Aviary studies

We and our students also studied blue grouse in aviaries (Zwickel and Bendell 1967*b*; Stirling and Bendell 1970; Danskin 1973; Cooper 1977), in both field and laboratory situations. Much of this work was oriented toward the identification of population processes, to be considered in a future publication. Nevertheless, we use some aviary data in this work to provide information that is not available from field studies, e.g., a description of copulation (15.2.3(h)), and determination of the secondary sex ratio (18.2.1(a)).

2.2 Approaches used in this book

2.2.1 Scope

This book is principally descriptive, an attempt to document what is known about the general biology and natural history of blue grouse. It leans heavily on information from our research in British Columbia and elsewhere. We have tried to be comprehensive, however, and include comparative information from all major studies of the species. There is an extensive "invisible" literature on this bird in the form of unpublished government reports, undergraduate and graduate theses and dissertations, and class projects. This literature often contains useful information on biology and natural history, and we have taken the liberty of citing from it if relevant and more than 10 years since completion. If more recent, we have contacted authors for permission before doing so.

2.2.2 Scientific nomenclature

In most cases scientific names of plants follow Hitchcock and Cronquist (1973) or Pojar and Mackinnon (1994). Those of reptiles follow Nussbaum et al. (1983); of birds, the AOU *Checklist of North American Birds* (AOU 1998) and AOU (2000); and of mammals, Nagorsen (1990).

Because of a plethora of common names that have been applied to the different subspecies of blue grouse, we refer to them by their scientific names. We use the full trinomial, e.g., *D.o. pallidus*, in most cases, but if clear, may use only the subspecific name in a following nearby reference.

2.2.3 Endnotes

We have made extensive use of Endnotes, for many of the data here have not been published and require some indication of methods used in their collection, or other clarifications. They are identified in the text by superscript numbers and appear at the end of each chapter.

2.2.4 Statistics

We used only commonly applied and standard parametric and non-parametric statistical tests to help evaluate our presentations in most cases, e.g., t test, analysis of variance, G test, Mann–Whitney U test, linear regression, etc. Confidence intervals (95%) for percentages in some graphs were calculated from the binomial distribution (Haddon 2001). We consider significance as $p \leq 0.05$ but think $0.10 > p > 0.05$ may be suggestive of significance were larger samples available and present p values as such if within this range. Test results are identified by numbers in square brackets in the text and appear by chapters in Appendix 1.

We are aware of the controversy over the use of significance tests (Johnson 1999; Anderson et al. 2000; Anderson et al. 2001; Robinson and Wainer 2002) but think many readers will want to see them applied to our data. There are many, and if you do not believe in their use, feel free to ignore them and evaluate our data and (or) conclusions as you wish.

Endnotes [Chapter 2]

1. Dogs were important in our work. Their sense of smell increases the efficiency of finding live and dead birds, nests, etc. They were used at all of our principal study areas except Lower Quinsam.
2. Blue grouse can be readily separated into three age classes, juveniles (juvs), yearlings (ylgs), and adults (ads), by characteristics of plumage when in the hand (Braun 1971). See glossary for defining characters.
3. In 1970 some removal birds were used for experimental introductions onto grouse-free islands (Bergerud and Hemus 1975).

4. In some cases, removal birds may not represent the general population, e.g., presumed "surplus" yearlings (Zwickel 1980). Necropsy data from these birds were not used for general descriptive purposes.
5. Thermographs were housed in small, natural wood "screens" at grouse (ground) level. Rain gauges, also were at grouse level, with tops of the collecting collars at ~20 to ~25 cm above the ground.

CHAPTER 3

Principal Studies and Study Areas

> *. . . there is a need for studies at intermediate to large spatial scales . . .*
> *[a] fruitful approach is to undertake parallel studies of the same species*
> *in different places using common methods.*
>
> Jamie Smith (1998)

Throughout this work we refer to a number of studies and study areas that have provided major contributions to our understanding of the natural history and biology of blue grouse. Here we provide a brief introduction to these studies and the areas in which they took place. We also introduce a number of mainly laboratory investigations. A third source of material is from the examination of museum specimens and a fourth from examinations of grouse shot by hunters. Museum specimens and birds shot by hunters are used to evaluate autumn sex and age ratios and provide data on other life-history traits. For quick reference, areas, subspecies involved, and principal investigators are summarized in Table 3.1.

Because of important differences in morphology, behaviour, and habitats of coastal and interior subspecies of blue grouse, we introduce field studies in relation to these two geographic classifications. More detail about some areas is provided in Chaps. 7 and 16. Figure 3.1 identifies approximate locations of the principal research areas and hunting season checking stations.

3.1 Coastal field studies

Most studies considered here involved *D.o. fuliginosus*. A major strength is that they involved intensive banding and census, in several cases over relatively long periods of time, i.e., ≥5 years. Also, methods have been relatively consistent among studies. A weakness is that most were conducted in British Columbia and are geographically limited, with only two short-term studies of *D.o. sierrae*, one of *D.o. sitkensis*, and one of *D.o. howardi*.

3.1.1 Lower Quinsam, BC

Fowle (1944) was first to study coastal blue grouse, *D.o. fuliginosus*, in any detail, 1942–1944. His research area was relatively flat or gently undulating, at a mean elevation of ~150 m (~120 to ~200 m) and near Lower Quinsam Lake, on eastcentral Vancouver Island. This was a descriptive study and emphasized summer habitat, the breeding cycle, diseases and parasites, food habits, and damage to forest plantations. No birds were banded.

Vegetation there is intermediate between the Coastal Douglas-fir and Coastal Western Hemlock Biogeoclimatic Zones (Anonymous 1985). This area was logged by clear-cutting, beginning as early as 1927, and was part of 30 000 ha burned by wildfire in 1938. At the time of study the vegetation was dominated by herbs, low shrubs, and Douglas-fir (*Pseudotsuga menziesii*) plantations <1 m tall.

Bendell (1955*c*) went to Lower Quinsam in 1950 to study parasitism in blue grouse, a response to a suggestion by Fowle and others that parasites might be a limiting factor to populations. With time, Bendell's objectives broadened to include the life history, ecology, and behaviour of this bird. Most adult males, yearling and adult females, and some yearling males and juveniles on two 15-ha census plots were individually colour-banded. This allowed Bendell to provide the first estimates of some demographic parameters of this bird, e.g., sex and age ratios, mortality rates, etc. More extensive search was done over an area of ~10 km^2. Intensive studies ended in 1953, with some follow-up in 1958 and 1959. Succession was much advanced relative to the time of Fowle's study, and the vegetation was composed of a broad mix of herbs, shrubs, and small Douglas-fir trees (plantations), but with large areas of open space.

3.1.2 Middle Quinsam, BC

In 1958 Bendell resumed intensive studies of blue grouse at Middle Quinsam Lake, ~10 km west of Lower Quinsam. A principal objective was to test hypotheses developed in his earlier work, especially those which suggested parasites were an important limiting factor and that production of young determined breeding density. The parasite hypothesis was rejected for this population, and Bendell, now joined by a number of colleagues, began long-term research that included population responses to habitat (Bendell and Elliott 1966), nutrients (Ash and Bendell 1978), and manipulations of density (Bendell et al. 1972). Numerous graduate and undergraduate studies were completed there, or involved laboratory or aviary work with birds from there. Most resident yearling and adult grouse and some juveniles were individually colour-banded on the principal study plots. Many grouse were collected for food habits, reproductive, and other investigations, mainly from surrounding areas or in conjunction with removal studies.

Middle Quinsam is in the same Biogeoclimatic Zone as Lower Quinsam and was burned by the same 1938 wildfire.

Table 3.1. Principal study areas, subspecies involved, and principal investigators.

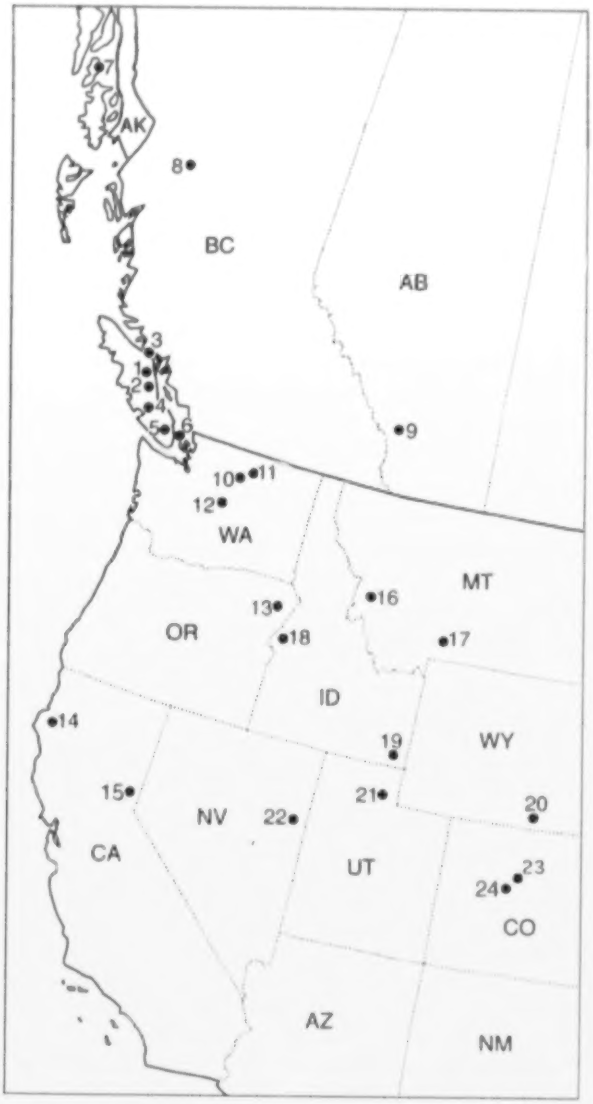
Areas	Subspecies	Principal investigators
COASTAL FIELD STUDIES		
Lower Quinsam, BC	*D.o. fuliginosus*	JF Bendell, CD Fowle
Middle Quinsam, BC	*D.o. fuliginosus*	JF Bendell
Comox Burn, Tsolum Main, BC	*D.o. fuliginosus*	FC Zwickel, JF Bendell
Mt. Washington, Brown's and Becher mts., BC	*D.o. fuliginosus*	DG King
Hardwicke Island, BC	*D.o. fuliginosus*	FC Zwickel
Ash River, BC	*D.o. fuliginosus*	JA Redfield
Copper Canyon, BC	*D.o. fuliginosus*	DH Mossop
Gulf Islands, BC; Stuart Island, WA	*D.o. fuliginosus*	AT Bergerud
May Ranch, CA	*D.o. fuliginosus*	FC Zwickel, MA Degner
Sage Hen Creek, CA	*D.o.* sierrae	RS Hoffmann
California	*D.o. sierrae*	JD Bland
Thomas Bay, Mitkof and Kuiu islands, AK	*D.o. sitkensis*	JG Doerr
INTERIOR FIELD STUDIES		
Conconully, WA	*D.o. pallidus*	L Wing, J Beer, W Tidyman
Skalkaho, MT	*D.o. pallidus*	TW Mussehl, P Schladwiler, RR Martinka, FC Zwickel, DT McKinnon
Frazer Creek, WA	*D.o. pallidus*	KM Standing, UB Henderson, RD Bauer, FC Zwickel
Cuddy Mt., ID	*D.o. pallidus*	EB Caswell, GC Heebner
Bridger Mts., MT	*D.o. pallidus*	TW Mussehl
Bear River Range, ID	*D.o. pallidus*	DF Stauffer
Miller Ridge, OR	*D.o. pallidus*	EC Pelren
Sheep River, AB	*D.o. richardsonii*	DA Boag
Hudson Bay Mt., BC	*D.o. richardsonii*	FC Zwickel, MA Degner
Green Mt./Eiby Creek, CO	*D.o. obscurus*	RW Hoffman
Middle Park, CO	*D.o. obscurus*	BS Cade, TE Remington
Centennial Ridge, WY	*D.o. obscurus*	HJ Harju
Liberty, UT	*D.o. obscurus*	DA Weber
Duck Creek, NV	*D.o. oreinus*	FC Zwickel, DT McKinnon
LABORATORY STUDIES		
University of British Columbia	*D.o. fuliginosus*	IG Stirling, JF Bendell
University of Toronto	*D.o. fuliginosus*	CR Cooper, JF Bendell
Utah State University	*D.o. obscurus*	PJ Pekins
Colorado State University	*D.o. obscurus*	TE Remington
MUSEUM SPECIMENS	All subspecies	JF Bendell, FC Zwickel
SAMPLES FROM HUNTERS		
Vancouver Island, BC	*D.o. fuliginosus*	JF Bendell, FC Zwickel
Washington	*D.o. pallidus*	FC Zwickel, JH Brigham
Colorado	*D.o. obscurus*	RW Hoffman
Idaho	*D.o. pallidus*	University of Idaho, Idaho Dept. Fish and Game staff
Montana	*D.o. pallidus*	TW Mussehl, P Schladweiler

The main study area was gently undulating, at elevations between ~275 and ~370 m. A portion of the area was burned by a second wildfire in 1952, providing two sharply contrasting seres: one, 20 years since burning (1938) and dominated by dense Douglas-fir plantations; the other, 6 years since burning and dominated by herbs, low shrubs, and small trees. This area was chosen for study in large part because of the opportunity for experimental manipulations (Bendell and Elliott 1966) provided by these contrasting seres. In 1978, at the termination of field work there, the entire area was dominated by dense or very dense Douglas-fir plantations.

3.1.3 Comox Burn and Tsolum Main, BC

(a) *Comox Burn*. In September 1961 a wildfire burned through some 40 km^2 of young second-growth forest that had been logged by clear-cutting, northwest of Courtenay on eastcentral

Fig. 3.1. Locations of principal study areas and hunting season checking stations: (1) Lower and Middle Quinsam; Campbell River, BC, (2) Comox Burn; Brown's and Beecher mts., Mt. Washington, BC, (3) Hardwicke Island, BC, (4) Ash River, BC, (5) Copper Canyon, BC, (6) Gulf, BC, and San Juan, WA, islands, (7) Thomas Bay, Mitkof and Kuiu islands, AK, (8) Hudson Bay Mt., BC, (9) Sheep River, AB, (10) Frazer Creek, WA, (11) Conconully, WA, (12) Chumstick, WA, (13) Miller Ridge, OR, (14) May Ranch, CA, (15) Sage Hen Creek, CA, (16) Skalkaho, MT, (17) Bridger Mts., MT, (18) Brownlee, ID, (19) Bear Range, ID, (20) Centennial, WY, (21) Liberty, UT, (22) Duck Creek, NV, (23) Green Mt., Whitely Peak, and Middle Park, CO, (24) Eiby Creek, CO.



Vancouver Island. In spring 1962, we began work there on a 485-ha portion of the burn, Comox Burn, as a principal study area (Zwickel and Bendell 1967*b*). We compared field and aviary survival of young grouse there to those at Middle Quinsam (10–12 years post-burning) from 1962 to 1964. Most resident adult and yearling grouse and some juveniles were individually colour-banded. Less intensive censusing and banding were carried out at Comox Burn from 1965 to 1968, mainly in connection with two graduate programs (Lance 1967; Mossop 1971). Experimental population removal studies, including five graduate programs, were begun in 1969 and continued through 1978, with the original study area serving as a control plot.

Comox Burn is in the same Biogeoclimatic Zone as Lower and Middle Quinsam. Topographic relief is greater than at Lower and Middle Quinsam, but relatively gentle (~240–460 m in elevation). In spring 1962, most of the area was barren of vegetation and dominated by stumps, charred remnants of larger logging debris, bare mineral soil, and ash. The fire of 1961 had burned most of the humus and smaller logging debris. In 1978, the last year of intensive field work there, many herbs and shrubs had been crowded out by Douglas-fir plantations that averaged 3–4 m in height.

(b) *Tsolum Main.* An experimental population removal plot, Tsolum Main (625 ha, 2–3 km north of the original Comox Burn study area) was established in 1969 and censused through 1977. Removal studies were designed to test hypotheses about the availability of "surplus" birds in spring. In general, we use "Comox Burn" as a generic term for the entire area, including the original plot (our control plot, (a), above). Tsolum Main was separated from the control plot by a "buffer area" (654 ha), and it and ~900 ha surrounding the other three sides of Tsolum Main were monitored for some purposes. We now identify the control plot as Comox Burn$_{cp}$ if reference is only to that area. Elevations, including all subunits, ranged from ~240 to ~680 m. Topographic relief was somewhat greater than at Lower and Middle Quinsam, but relatively gentle. Most resident adult and yearling grouse and some juveniles were individually colour-banded in non-removal years. Many birds were collected in conjunction with removals.

About one-half of Tsolum Main was burned by the same wildfire as at Comox Burn$_{cp}$, and by 1969 virtually all of the remaining area had been logged by clear-cutting. Plant succession was slightly behind that on the control plot because of a slightly higher elevation and the post-fire logging of some unburned areas.

3.1.4 Mount Washington, Brown's and Becher mountains, BC

Mount Washington and Brown's and Becher mountains are adjacent to Comox Burn and serve in part as winter range for birds from there. King (1971) studied grouse year round, from May 1965 to June 1966, on three areas between ~1000 and ~1500 m in elevation, totalling ~23 km^2, and comprising upper elevations of these mountains. Principal objectives were to study birds on winter range and to compare the demography and habitat use of grouse living year round in subalpine habitat to that of birds breeding in nearby lowlands. Few birds were banded, and many analyses were based on collected birds.

Most of King's work was in subalpine forest, in the Mountain Hemlock and Alpine Tundra–Mountain Hemlock Biogeoclimatic Zones (Anonymous 1985). Mountain hemlock (*Tsuga mertensiana*) forest was dense at lower elevations (1000–

1200 m) with scattered clumps of trees amid mountain meadows (parkland), cliffs, and rock outcrops at upper elevations (>1200 m). Deep valleys separated the three study areas.

3.1.5 Hardwicke Island, BC

This island of ~77 km^2 lies between Vancouver Island and mainland British Columbia. We chose this area to try to limit dispersal movements. Our major objective was to examine over-winter survival and subsequent recruitment of juveniles into the breeding population. In 1979, most yearling and adult birds and many juveniles were individually colour-banded on a principal plot of 465 ha. Smaller chicks were marked with patagial wing tags. Many grouse, especially juveniles, were equipped with radios and monitored in springs and summers through 1984. Radio-equipped birds were studied in the winters of 1979–1980 through 1981–1982 (Hines 1986*b*, 1987).

Hardwicke Island is in the Coastal Western Hemlock Biogeoclimatic Zone (Anonymous 1985). Topography of the main census plot was very broken and ranged from gentle to very steep, at elevations from ~180 to ~450 m. Maximum elevation on the island was ~800 m. By 1979, much of the island had been burned by wildfire or logged by clear-cutting, beginning around the turn of the century. Most of the forest was in advanced stages of succession, i.e., ≥20 to >80 years post-logging or burning, with old-growth largely restricted to higher elevations. The main study plot was located centrally in the largest single block of young seral stages (<15 years post-logging). Parts had been planted to Douglas-fir (mainly), but much of the regeneration was volunteer western hemlock (*Tsuga heterophylla*). Herbs and shrubs dominated the understory. By 1984, succession had advanced to the point where some areas were difficult to walk through.

3.1.6 Ash River, BC

In 1968, Redfield (1973*a*) began a study of colonization of newly logged forest by blue grouse in the Ash River Valley on westcentral Vancouver Island. He was particularly interested in the genetics of recruits to newly logged sites and worked three plots totalling 908 ha. Field work terminated in 1971. Most resident yearling and adult grouse and some juveniles were individually colour-banded.

This valley is in the Coastal Western Hemlock Biogeoclimatic Zone (Anonymous 1985). Each study plot was composed of a mosaic of young seral stages (<1 to >8 years post-logging) that ranged from 15 to 40 ha in size. Elevations of the plots ranged from ~200 to ~1100 m. All had been planted with Douglas-fir, with plant structure related to specific sites and time since cutting and planting. Douglas-fir and western hemlock were the principal conifers.

3.1.7 Copper Canyon, BC

Copper Canyon is on southeastern Vancouver Island. In 1967 and 1968 Mossop (1971) compared the behaviour of grouse there, a "dense" population, to that of grouse at Middle Quinsam and Comox Burn, where densities were moderate to low. His principal objective was to test the hypothesis that social behaviour does not differ in populations with different densities. He had a 17-ha census plot but studied and conducted behavioural experiments over an area of ~650 ha. Elevations ranged between ~450 and ~750 m. This area is relatively steep and dissected by "numerous drainage gullys" (Mossop 1971, p. 7). Birds were very wild and few were banded.

Vegetation was generally similar to that at Lower and Middle Quinsam and Comox Burn. The study area had been logged by clear-cutting, then planted with Douglas-fir. At the time of study, the vegetation consisted mainly of mixtures of herbs, low shrubs, and Douglas-fir of 1–10 years of age (Mossop 1971).

3.1.8 Gulf Islands, BC, and Stuart Island, WA

In 1970, Bergerud and Hemus (1975), and we, captured grouse at Copper Canyon, Middle Quinsam, and Comox Burn for experimental introductions onto three of the Gulf Islands (Moresby, Sidney, and Portland, BC) and Stuart Island, WA, between Vancouver Island and the mainland coast. All were grouse-free. The principal objective was to compare demographic and behavioural responses of birds from populations of different densities when placed together, and in isolation, an effort to sort out innate from extrinsic influences on populations and behaviour. As well, Donaldson and Bergerud (1974) censused and studied behaviour and habitat selection of a resident population of blue grouse on nearby Prevost Island.

The Gulf Islands are continuous with the northern San Juan Islands in Washington State (Stuart Island is in the San Juan group). Four of the Islands on which grouse were studied are <700 ha in size (Sidney Island is 932 ha) and few points exceed 100 m in elevation. All are in the Coastal Douglas-fir Biogeoclimatic Zone (Anonymous 1985). Much of the forest habitat had been subjected to selective logging; and some of the islands, to grazing by domestic animals, mainly sheep. All of the above studies involved *D.o. fuliginosus*.

3.1.9 May Ranch, CA

In 1985, we studied *D.o. fuliginosus* on a 696-ha plot on the Eleanor May Ranch at Bridgeville in northwestern California. This is near the southern end of the range of this subspecies. The study area was steep and ranged from ~200 to ~800 m in elevation. Slopes are generally south-facing and drop steeply into the Van Duzen River Valley. Demographic and behavioural studies there were part of an attempt to compare these attributes in selected areas throughout the range of blue grouse to those from our long-term studies in British Columbia. In short, we attempted to identify demographic and behavioural generalities that might, or might not, exist at the species level. Grouse were wary and difficult to capture, and few were individually marked. See 7.4.1(c) for detail on vegetation of this area.

3.1.10 Sage Hen Creek, CA

Hoffmann (1956) worked with *D.o sierrae* in eastcentral California. He studied the behaviour and demography of a small isolated population on the east slope of the Sierra Nevada and did some analyses of the quality of their winter food (Hoffmann 1961). No birds were banded.

The study area there, ~1 km^2, and at an elevation of ~2100 m, was mostly forested, with white fir (*Abies concolor*) the predominant tree. Less common trees included red fir (*Abies magnifica*), Jeffrey pine (*Pinus jeffreyi*), and western white pine (*Pinus monticola*), with lodgepole pine (*Pinus contorta latifolia*) and trembling aspen (*Populus tremuloides*) on some sites. The forest was relatively open and can best be described as xeric and interior-like.

3.1.11 California

In the spring and summer of 1992, Bland (1992, 1993, 1997) worked with, and developed a plan for monitoring, *D.o. sierrae* in California. He identified hooting (singing) groups of territorial males to estimate and establish an index for monitoring densities over the range of this bird within the state. Habitats occupied by territorial males were described, and no birds were banded. More recently he began a search for remnant birds in insular populations of *D.o. howardi* (Bland 2002, 2003).

3.1.12 Thomas Bay, Mitkof, and Kuiu islands, AK

Densities of territorial male *D.o sitkensis*, and their use of habitat, were documented at the three areas above in southeast Alaska in 1980 and 1981 (Doerr et al. 1984). Objectives were to compare population densities and habitat preferences of males between old-growth and clear-cut forests.

Old-growth forest was uneven-aged and dominated by western hemlock and Sitka spruce (*Picea sitchensis*), with varying amounts of other conifers. The overstory canopy generally exceeded 65%. A well-developed understory was dominated by deciduous shrubs, broad-leaved herbs, and ferns (Polypodiaceae). Clear-cuts examined ranged in age from 1 to 23 years since logging, with a high production and diversity of deciduous shrubs and herbs. Approximately 1360 ha of old-growth and 1900 ha of clear-cuts were searched for singing males on various sized plots.

3.2 Interior field studies

In contrast to studies of coastal grouse, those of interior birds have involved a broad spectrum of long- and short-term studies of all local subspecies. A weakness is that observers, methods, and intensities of study often differed, making it difficult to compare some features of grouse and their habitats among interior, and to coastal, populations.

3.2.1 Conconully, WA

Wing et al. (1940) were first to undertake intensive field work with blue grouse, in this case, *D.o. pallidus*. Principal objectives were to document life history and ecological attributes of the species. Methodology was mainly observational but was supplemented by collecting birds. No grouse were banded. This work involved the summer of 1940 only, and birds were studied in both breeding and winter habitats.

Wing et al. ranged over an area of perhaps 500 km^2. This area is on the east-facing slope of the Cascade Mountains in northcentral Washington and elevations ranged from ~460 to >2500 m. "The topography is rough and consists of sharp slopes terminating in peaks and ridges" (Wing et al. 1940, p. 5). Plant formations ranged from Daubenmire's (1946) Wheatgrass–Bluegrass Zone to his Tundra Zone.

3.2.2 Skalkaho, MT

A long-term study of *D.o. pallidus* was begun in 1962 on a 477-ha plot in the Skalkaho Creek drainage, western Montana (Mussehl 1963*b*). This area is steep, ranges between ~1400 and 1900 m in elevation, and consists mainly of two north–south trending ridges. Studies were principally of a descriptive demographic nature, with birds there also serving as a control population for experimental studies of the effects of insecticide spraying on grouse in nearby forest (Mussehl and Finley 1967; Mussehl and Schladweiler 1969). Intensive field work was terminated in 1967 (Mussehl et al. 1969). Many adult males, and presumably many adult and yearling females, were individually colour-banded.

In 1968 and 1969, Martinka (1972) studied how territories of adult males related to vegetation structure on the same study area used by Mussehl and co-workers. Most territorial males were individually colour-banded.

In 1986, we worked in this area for this one breeding season, as part of our studies of birds in various parts of their range. About 30% of the resident yearling and adult males and females and some juveniles were captured and individually colour-banded. Some smaller chicks were marked with patagial wing tags. Our plot encompassed most of the study area of Mussehl, Schladweiler, and Martinka, plus a little more. See 7.4.2(c) for more detail on vegetation of this area.

3.2.3 Frazer Creek, Methow Valley, WA

From 1956 to 1961, three graduate studies of *D.o. pallidus* were conducted on the 40 km^2 Methow Game Range and vicinity, in the Methow Valley, northcentral Washington (Standing 1960; Henderson 1960; and Bauer 1962). A principal plot of ~260 ha, Frazer Creek, was used for intensive banding and some census work. Mean elevation of the study plot was ~900 m. Standing's principal objectives were to investigate reproductive parameters as they might relate to demography. Henderson and Bauer emphasized the study of broods in mid to late summer, especially their movements, sex and age composition, behaviour, and use of habitat. Grouse were marked with numbered aluminum bands, mainly at Frazer Creek.

In 1968, we studied the effects of grazing by domestic cattle on grouse, using the ungrazed Frazer Creek area as a control plot (Zwickel 1972*b*). We compared birds there to those on a nearby heavily grazed plot, of ~235 ha, at Balky Hill, ~5 km to the west. Principal objectives were to examine the effects of grazing on breeding densities, reproductive success, and habitat selection. Some birds were individually colour-banded.

The Methow Game Range lies along the west-facing foothills of an eastern outlier range of the Cascade Mountains. The Frazer Creek and Balky Hill study plots are in the Wheatgrass–Bluegrass Zone (Daubenmire 1946), as is most of the Game Range. Structurally, this habitat can be described as shrub-steppe. It was dominated by two shrubs, bitterbrush (*Purshia tridentata*) and big sagebrush (*Artemisia tridentata*), and a mix of bunchgrasses (Gramineae) and xeric herbs. Widely scattered thickets of trembling aspen and ponderosa pine (*Pinus ponderosa*) were present, mainly in the bottoms of draws.

3.2.4 Cuddy Mountain, ID

Two successive graduate studies of *D.o. pallidus* were conducted on Cuddy Mountain in the Brownlee drainage, west-central Idaho (Caswell 1954*b*; Heebner 1956). Caswell spent a full year in the field, beginning in May 1952. His was a descriptive natural history and ecology study. Heebner was in the field in the springs, summers, and early autumns of 1954 and 1955. His main objectives were to study nesting and brood habits, to evaluate nesting range, and to develop a census method. As far as we can tell, no grouse were banded in either study.

Caswell ranged over an area of some 80 km^2 but did more intensive censusing on a plot of 260 ha. Most breeding season observations were made at elevations between ~1000 and 1350 m, and winter observations, between ~1600 and 1950 m. Heebner's studies were concentrated between ~1070 and 1500 m.

The Spruce–fir, Douglas-fir, Ponderosa Pine, Wheatgrass–Bluegrass, and Sagebrush–Grass Zones (Daubenmire 1946) were all represented in areas worked by Caswell. Heebner worked mainly in the latter two zones, the principal summer range for grouse in this region.

3.2.5 Bridger Mountains, MT

D.o. pallidus were studied by Mussehl (1960) in the Bridger Mountains, ~30 km north of Bozeman in 1957 and 1958. This was a general life history and ecology study, with emphasis on movements, broods, and population characteristics on breeding range. Many birds were captured and individually colour-marked.

The main study area consisted of ~26 km^2 on a west-facing slope of the Bridger Mountains. Mussehl reported (p. 61), "The slopes are generally steep." Elevations ranged from ~1600 to 2700 m. Montane Douglas-fir forest was the principal vegetation type at upper elevations. Immediately below was a shrub-steppe community dominated by big sagebrush and bitterbrush. Bunchgrass prairie extended downward from there.

3.2.6 Bear River Range, ID

Stauffer (1983) examined seasonal habitat selection by *D.o. pallidus* in the Bear River Range of southeastern Idaho from 1978 to 1981. Twenty-one line transects were located over an area of ~1080 km^2 in the Caribou National Forest. Birds were censused by walking transects and habitats in which grouse were found were described. No grouse were banded.

Stauffer classified vegetation on the overall study area into eight types. Four at lower elevations were dominated by shrubs, with the remainder in forest. Forested communities graded upward from a seral "aspen type", through "dense conifer", to an "open conifer type" on higher ridges and slopes (Stauffer 1983). Elevations ranged from ~1580 to 2950 m.

3.2.7 Miller Ridge, OR

Winter ecology of radio-marked *D.o. pallidus* was studied at Miller Ridge in northeastern Oregon by Pelren (1997) in the winters of 1991–1992 through 1993–1994. Principal objectives were to document movements from summer to winter range, to examine winter habitats, to estimate over-winter survival, and to compare these factors among sex and age groups. A secondary study included a documentation of nesting parameters and their habitat associations (Pelren and Crawford 1999).

Grouse were captured, banded (aluminum bands only), and in most cases equipped with radios, on an area of ~10 km^2, between ~950 and 1500 m in elevation. North-facing slopes were dominated by Douglas-fir and ponderosa pine, south-facing slopes by bunchgrass meadows.

3.2.8 Sheep River, AB

Boag (1966) was first to undertake a long-term study of interior grouse, in this case, *D.o. richardsonii*. Intensive research was conducted on a plot of ~250 ha from 1956 to 1962 in the Sheep River drainage, southwestern Alberta. Less intensive censusing continued through 1974. Principal objectives were to describe the demography and general ecology of birds in this region. Many were individually colour-banded in years of intensive study.

This study area was in the southeastern foothills of the Rocky Mountains. Topography was moderate to steep, at elevations between ~1500 and ~1750 m. Vegetation consisted of a mosaic of three major plant associations: "closed-forest", dominated by white spruce (*Picea glauca*); "grassland", dominated by rough fescue (*Festuca scabrella*); and "rock-outcrop–open-forest", dominated by Douglas-fir. Open-forest was in various stages of seral succession, and parts were dominated by trembling aspen and lodgepole pine.

3.2.9 Hudson Bay Mountain, BC

D.o. richardsonii[1] inhabit this area in westcentral interior British Columbia. This was another population we studied for one breeding season (1986) for comparison to our long-term studies on Vancouver Island. About 50% of the adult and yearling males and females were individually colour-banded on a 550-ha area. Approximately 200 ha encompassed a downhill ski development.

Hudson Bay Mt. rises steeply from the Bulkley Valley, beginning at ~490 m and rising to 2409 m. Our study area, at ~1450–1750 m, was located on the southern and southeastern sides of the mountain and ranged from just below upper treeline (~1575 m) well into the alpine.

3.2.10 Green Mountain and Eiby Creek, CO

Hoffman (1981) studied *D.o. obscurus* at Green Mountain, near Kremmling, and at Eiby Creek, near Eagle (~40 km southwest of Green Mountain), from 1975 to 1980. Study plots were 181 and 482 ha in size, respectively. Principal objectives were to document demography, habitat relationships, and the effects of hunting on populations. These areas were chosen in part because they represented different habitat types. Green Mountain had extensive areas of conifer forest, while Eiby Creek had few conifers. Many grouse were individually colour-banded.

Green Mountain was typical of a mosaic shrub-steppe–conifer forest breeding range. The study plot included portions of the Sagebrush and Douglas-fir Zones (Harrington 1964) and ranged in elevation from ~2540 to 2870 m. Shrub-steppe was dominated by big sagebrush, bitterbrush, and xeric herbs. It occupied about 60% of the plot, with the remainder dominated by Douglas-fir (mainly) and trembling aspen.

Elevations at Eiby Creek ranged from ~1900 to ~2500 m. This area ". . . falls within a transition belt between the Pinyon–Juniper and Spruce–Fir Zones and consists of a mosaic of mountain-shrub, aspen, sagebrush, and riparian communities. Conifer types are virtually absent . . ." (Hoffman 1981, p. 110).

3.2.11 Middle Park, CO

Cade (1985) studied winter habitat use and migration of radio-marked grouse on Whitely Mountain and on Hoffman's Green Mountain study area, both in Middle Park, from April 1981 to November 1983. He was mainly interested in whether migration patterns and winter habitat selection differed among sex and age classes. Some grouse moved off the study areas in winter and were monitored less frequently than those that remained.

Cade described vegetation on the 503-ha Whitely Peak site as about 27% conifer forest, 23% trembling aspen forest, and 50% non-forested [shrub-steppe]. Douglas-fir dominated the conifer forest and sagebrush, the shrub-steppe.

3.2.12 Centennial, WY

Harju (1974) worked with *D.o. obscurus* in southeast Wyoming. He described several aspects of their general ecology from 1970 to 1973, emphasizing reproductive behaviour, use of habitat, and populations. Some birds were captured and individually colour-banded, but the proportion of the population marked was relatively small.

Grouse were studied on three separate areas. At Centennial Ridge work was concentrated on 260 ha (elevations ~2590–2960 m), with most of the plot in Hanna's (1934) Montane Zone. Principal conifers were subalpine fir (*Abies lasiocarpa*), Douglas-fir, and lodgepole pine. Trembling aspen were mixed within and at the edge of conifer stands.

A second site of about 65 ha (elevations ~2400–2500 m) was in the Centennial Valley, and a third, of ~260 ha (elevations ~2280–2400 m), in the Douglas Creek drainage. Both were in Hanna's (1934) Low Mountain Zone, with groves of mature trees and open shrub-covered hillsides (Harju 1974). Principal trees were subalpine fir, lodgepole pine, and trembling aspen.

3.2.13 Liberty, UT

D.o. obscurus were studied in northcentral Utah by a succession of graduate and undergraduate students from 1970 to 1974 (Weber 1975). A major objective was to document life history and ecological attributes of grouse, and, a second, to evaluate the effects of herbicidal spraying on populations. Some birds, mostly large juveniles, were captured, banded, and individually colour-marked with neck bands. A 330-ha main study area was rolling to hilly (Weber 1975) and between ~1890 and 2010 m in elevation. Shrubs, mainly big and black (*Artemisia nova*) sagebrush, dominated the landscape, with Douglas-fir on surrounding slopes.

3.2.14 Duck Creek, NV

We studied *D.o. oreinus* in the Duck Creek drainage, Schell Creek Range, in eastcentral Nevada in 1985. As at the May Ranch and Skalkaho, this was part of our attempt to seek generalities in various parts of the range of blue grouse. Grouse were very wary, and few individuals were captured and marked.

In Nevada, most grouse populations are disjunct, occurring in isolated mountain ranges separated by broad intermountain valleys. This was true for the Schell Creek Range. We worked on a 690-ha plot consisting mainly of two gently rolling ridges and ranging from ~2360 to 2650 m in elevation. This was a shrub-steppe breeding range, most of which was dominated by big sagebrush. See 7.4.2(a) for more detail.

3.3 Laboratory studies

3.3.1 University of British Columbia (UBC), Vancouver, BC

Birds raised from eggs collected at Middle Quinsam and Comox Burn, or captured as young chicks, were maintained in an aviary at UBC. Principal objectives were to develop methods of holding and rearing grouse in captivity and to study their behaviour and nutrition (Stirling 1965). Two graduate programs involving parasitism (Jensen 1962; Gibson 1965) were also completed there.

3.3.2 University of Toronto (UT), Toronto, ON

Birds from Middle Quinsam and Comox Burn were also maintained at UT. Principal objectives were to further develop methods of holding and rearing grouse in captivity, to describe their behaviour in captivity, and to compare behaviours of those from dense to those from sparse populations, especially as they related to theories of population regulation (Cooper 1977, continued by Bendell).

3.3.3 Utah State University (USU), Logan, UT

Winter energetics of *D.o. obscurus* were studied at USU (Pekins 1988). Energetics and metabolism were examined under laboratory conditions (of birds taken from the wild) and in the field. These data were related to winter climates and habitats to which local populations were exposed. Potential energy saving behaviours of birds were examined in the field.

3.3.4 Colorado State University (CSU), Fort Collins, CO

Winter food selection and nutritional ecology of *D.o. obscurus* were studied by Remington (1990) under laboratory conditions. Food habits also were examined by observing radio-marked birds in the wild and by food selection and nutrition experiments in the laboratory (with birds taken from the wild).

3.4 Museum specimens

We examined 2313 specimens for age and sex in 34 museums across North America. We recorded dates and areas of collection, selected information from plumages (e.g., sexes and ages), and other information that might accompany the specimens. Specimens date back to the 1800s, represent a composite sample from different areas and years, and are, of course, subject to biases of the collectors.

3.5 Samples from hunters

Hunters provide an opportunity to examine age and sex ratios among grouse shot in autumn. Such analyses provide the only demographic information available for some populations but must be used with caution. If used judiciously and in conjunction with other data, they may provide insights into the vulnerability of age and sex classes of grouse to hunters (Bendell and Elliott 1967; Zwickel et al. 1975; Hoffman 1985), the natural history of grouse, e.g., food habits (Boag 1963; Crawford et al. 1986*b*), reproductive success (Braun 1971; Hannon 1981; Cedarleaf et al. 1982; Crawford et al. 1986*a*), and movements (Zwickel et al. 1968). An advantage of such data is that samples can be large and can provide simultaneous collections of data over relatively large areas.

Wings and tails, for determination of sex and age (Mussehl and Leik 1963; Braun 1971; Nietfeld and Zwickel 1983), have often been collected at checking stations where virtually all birds killed within a specific area and time period were examined. These are likely the most useful samples from shot birds for population analyses, especially if data from other studies in the same area are available.

Wings from shot birds also have been collected at volunteer "wing barrels" (Hoffman 1985). This is sometimes the only practical method of sampling populations but has two important weaknesses: (1) less is known about the source of the samples, and (2) biases may be introduced by differential submission of sex and age classes by hunters. A third source of samples involves asking hunters to submit wings through the mail, "mail-in" surveys (Hoffman 1985). This has the same drawbacks as the latter, perhaps accentuated. Despite problems with these methods, they often provide large samples over larger areas than can be collected at checking stations, are less labour intensive, and provide information for comparison among areas and years.

3.5.1 Vancouver Island, BC (D.o. fuliginosus)

Grouse shot by hunters have been examined at various checkpoints on Vancouver Island over a wide span of time. In most cases, these were from the opening weekend of the grouse season only, usually late August or early September. This is the period during which the greatest kill takes place. Virtually all wings, and in many cases, tails, were collected from grouse brought through checkpoints, beginning in 1962. Sexes and ages of most were verified by one of us. All areas but one (Ash River) from which samples were collected are on the eastern slope of Vancouver Island.

(a) *Campbell River.* Grouse were first examined in 1949 at a checkpoint at Campbell River (Taylor 1951), and through 1964. From 1949 through 1961, sexes and ages were classified by a variety of different persons, in most cases at the checkpoint. We use only data for the period 1962–1964 for our analyses, i.e., those for which wings and tails were collected and for which we verified sexes and ages. Some of the earlier data are included in unpublished (Taylor 1951; Robinson 1953; Hockin 1967), or published (Hatter 1955; Redfield et al. 1970), reports.

Birds checked at Campbell River came from a region of ~800 km^2. The Lower and Middle Quinsam study areas are both located within this area, and their descriptions characterize the general region where most hunting took place.

(b) *Courtenay.* Wings and tails were collected from virtually all birds examined at a checkpoint near Courtenay from 1970 to 1979 (except 1974). The region sampled was ~250 km^2 (Zwickel 1982). Comox Burn was within this region and was the principal area in which grouse were hunted. Its description characterizes sites from which most birds were taken. Mount Washington and Becher and Brown's mountains represent higher elevations within this region.

(c) *Ash River.* BR Simard collected wings and tails in this watershed in 1964. This region (~200 km^2) includes the study areas later used by Redfield (1973*a*). Most grouse were taken in habitats typical of Redfield's study plots. Few elevations accessible to hunters might exceed 1000 m, and upper elevations are generally similar to those on Mount Washington and Brown's Mountain.

(d) *Chemainus River.* We collected wings and tails from a region of ~200 km^2 in the Chemainus River watershed in 1964. The country is steep and rugged and includes the Copper Canyon study area of Mossop (1971). Some elevations exceed 1500 m. The description of Copper Canyon characterizes most of the region from which grouse might have been taken. Earlier samples from here were examined by personnel of the BC Wildlife Branch (Taylor 1951; Robinson 1953).

(e) *Cumberland.* JD Vanada collected wings and tails from an area of ~80 km^2 in the Trent River watershed in 1972. Elevations range from near sea level to >1000 m. This area is steeper and more rugged than, but vegetatively similar to, Comox Burn (~15 km to the northwest) and adjacent mountains.

3.5.2 Washington State (D.o. pallidus)

Grouse were examined at three locations in northcentral Washington: Chumstick and Conconully (Zwickel et al. 1975), and Eight Mile Creek, all on the east-facing slope of the Cascade Mountains. Wings and tails were collected from virtually all birds, with sexes and ages verified by Zwickel and JH Brigham.

(a) *Chumstick.* Grouse were checked there in all years 1953–1964. This area of ~250 km^2 ranges in elevation from ~460 to 1780 m. Plant communities range from Daubenmire's (1946) Wheatgrass–Bluegrass Zone to his Spruce–Fir Zone.

(b) *Conconully.* Conconully is ~120 km north of Chumstick, and birds were checked over the same period as there. The check area of ~250 km^2 ranges in elevation from ~460 to >2500 m. Plant communities range from Daubenmire's (1946) Wheatgrass–Bluegrass Zone to his Tundra Zone. Most birds were taken within the larger region worked by Wing et al. (1940), as described above.

(c) *Eight Mile Creek.* Wings and tails were collected from grouse shot in this region from 1959 to 1961. This area of ~200 km^2 included upper reaches of the Chewack River, a tributary of the Methow River. It is west of the Conconully region and borders on it. Elevations range from ~650 to >2500 m. In contrast to Chumstick and Conconully, the upper Chewack drainage is virtually all forested. Major plant communities range from Daubenmire's (1946) Douglas-fir Zone to his Tundra Zone.

3.5.3 *Colorado* (D.o. obscurus)

Wings were collected in Middle Park from 1975 to 1982, 87% from volunteer wing collection barrels (Hoffman 1985). Some were collected at checking stations (12%) or through mail-in surveys.

Middle Park, ~2000 km^2, is located on the west-facing slope of the Rocky Mountains. This is a large intermountain basin ranging in elevation from ~2200 to >3500 m and includes the Green Mountain and Whitely Peak study areas. Sagebrush communities dominate the landscape below 2700 m, conifer and aspen forest, above. In contrast to other mountain parks in Colorado, mainly dominated by sagebrush, Middle Park is heavily forested locally. Some upper elevations reach alpine tundra.

3.5.4 *Idaho* (D.o. pallidus)

University of Idaho staff and students and personnel of the Idaho Fish and Game Department examined grouse at various checkpoints throughout the state from 1952 to 1954 (Salter 1954; Heebner and Dalke 1955) and in 1958 (Bizeau 1958). This provided data on numbers of juveniles and of yearlings and adults combined, but no information on sexes. These data can be used to examine age ratios only. We combined data for all years and all areas to give a general picture of the age structure of grouse killed by hunters for the state.

3.5.5 *Montana* (D.o. pallidus)

Biologists of the Montana Fish and Game Department collected data on the age structure of birds shot by hunters through mail-in wing surveys and at checking stations in various regions of the state (Mussehl 1961, 1963*b*; Schladweiler 1968). Data were not separated by sex, and we combined data from all years and areas to give a general picture of age ratios for the entire state.

Endnote [Chapter 3]

1. Some birds here are likely hybrids between *D.o. richardsonii* and *fuliginosus*, but most closely resemble the former.

Part 2
Background to the Species

CHAPTER 4

Taxonomy and Distribution

4.1 Taxonomy

> *The great number and diversity of animals require some framework order within which they can be viewed.*
>
> Claude Villee et al. (1979)

4.1.1 Vernacular nomenclature

Vernacular, or common names, can cause problems of species identification, and some argue that only scientific nomenclature should be used to refer to species or races of animals (or plants). Idealistic as this may be, vernacular names are usually shorter, widely used, and, in our view, here to stay. The important point then is to identify the species to which one is referring when identified by a common name.

According to Johnsgard (1983, p. 363), the word "grouse" is "probably from the French, *greoche*, *greiche*, and *griais*, a spotted bird, and used in England as 'grous' for the red grouse [*Lagopus lagopus scoticus*] before being applied in North America to grouse in general."

(a) *Aboriginal and European vernacular names.* Local aborigines utilized blue grouse long before Europeans arrived in North America (see 6.1). Some aboriginal nations or groups appear to have referred to all grouse with one name and did not separate species. Others identified species with distinctly different names (Table 4.1), e.g., the Moses Columbia Language identified blue grouse, ruffed grouse (*Bonasa umbellus*), sage-grouse (*Centrocercus urophasianus*), sharp-tailed grouse (*Tympanuchus phasianellus*), and spruce grouse (*Falcipennis canadensis*) individually (Kinkade 1981). Some non-English European names applied to blue grouse are *gallo azul* (Spanish), *tetras sombre* (French), and *Felsengebirgshuhn* (German).

(b) *English vernacular names.* Many common names have been applied to blue grouse in the English literature. We document those we have found, some of which also may have been used for other species. Those of mainly a historical nature, most of which were used by only one or two authors, include the following: pheasant (Zebulon Pike, in Coues 1895*b*); fesant [sic], black pheasant, large black pheasant, black and white pheasant, large black and white pheasant, dark brown pheasant, large dark brown pheasant, speckled pheasant, and large dommanicker (Meriwether Lewis, in Moulton 1987, 1988*a*, *b*, 1991, 1993); mountain grouse, rock grouse, partridge, and black partridge (Douglas 1914); black-tailed grouse (Coues 1874), wood grouse and large wood grouse (Dawson and Bowles 1909; Dawson 1923), American capercaillie (Anonymous 1921), and black grouse (Dawson and Bowles 1909; Douglas 1914; Jewett et al. 1953). Names used more widely are dusky grouse, sooty grouse, fool grouse, fool hen, pine grouse, pine hen, gray grouse, and hooter. At the subspecific level other variations occur, e.g., Richardson's grouse (*D.o. richardsonii*), Sitkan grouse (*D.o. sitkensis*), and Sierra grouse (*D.o.sierrae*). The latter are sometimes made more specific by inserting "blue", "sooty", or "dusky" into the name, e.g., Richardson's blue grouse.

Blue grouse is the most widely used generic vernacular name to refer to all races of the species. Two other common generic terms are "dusky grouse" and "sooty grouse", often used to refer to four interior and four coastal subspecies, or to individual subspecies of each group, respectively.

Table 4.1. Some North American aboriginal names applied to blue grouse.

Name	Nation/group	Source
e-too-kum (i-tu-kum)	Yuki	Sawyer and Schlicter 1984
mo'xmuk^{u}t	Bella Coola	Boas 1898
muc·uma·s-y-	Northern Sierra Miwok	Callaghan 1987
OMAHKSSTSIIKITSSITSOM	Blackfoot	Frantz and Russell 1989
pistac'i	Gitskan	Maud 1982
qul-al-lalleun	Chinook	Audubon 1840–1844
səsə́q̇^{w}	Moses Columbia	Kinkade 1981
tuẏé	Nez Perce	Aoki 1994
tuyá	Yakama	Beavert and Rigsby 1975
tyee-culaw-culaw	Northwest coast	Bendire 1892

4.1.2 Scientific nomenclature

(a) *Order and family-level designations.* Blue grouse are in the avian Order Galliformes (from *gallus*, Latin word for cock (Johnsgard 1983)), often referred to as the scratching, or chicken-like birds. When first technically named (see below), all grouse were placed in the family Tetraonidae. Mayr and Amadon (1951), Brodkorb (1964), Vaurie (1965), and Short (1967), among others, have argued the grouse warrant recognition only as a subfamily, the Tetraoninae, within the family Phasianidae. This change was formalized in the sixth edition of the *Checklist of North American Birds* (AOU 1983) but has not been fully accepted by some, e.g., Potapov (1985) and del Hoyo et al. (1994). Principal external features separating grouse from other phasianids are the presence of feathered tarsometatarsi, feathers around the nostrils, and a seasonal presence of pectinations on the toes of most species[1] in winter.

(b) *Specific level designations.* Blue grouse were first technically named *Tetrao obscurus* (*obscurus*, Latin word for dusky (Johnsgard 1983)), the dusky grouse, by Thomas Say (in James 1823). As for many species, the scientific nomenclature has undergone many revisions, mostly at the subspecific level, and for detail see Ridgway and Friedmann (1946). We examine major highlights only.

In the late 1800s blue grouse were sometimes placed in the genus *Canace* (e.g., Baird et al. 1874; Ridgway 1877; Coues 1887), along with spruce grouse. *Tetrao*, however, dominated the literature well into the 1870s (Suckley 1860; Allen 1871; Coues 1874; Wilson and Bonaparte 1876, among others). Elliot (1864) proposed that *Tetrao* should be used only for capercaillie (*Tetrao urogallus*) and suggested blue grouse be placed in a new, monotypic genus, *Dendragapus* (from *dendron*, Greek word for tree, and *agape*, Greek word for love, lover of trees (Johnsgard 1983)). By the end of the nineteenth century this was generally accepted.

Following Say's description in the southern Rocky Mountains, Douglas (1829) described a new form from the northern Rockies, *Tetrao Richardsonii* (Fig. 4.1). This was recognized as a new species until Ridgway (1885) reduced it to subspecific status, *D.o. richardsonii*. Now only one species was recognized, but which included several races; one of which, *D.o. fuliginosus* (*fuliginosus*, Latin word for sooty (Johnsgard 1983)), a coastal form, had been identified by Baird and Ridgway (1873). This bird was raised to specific status in the fourth edition of the *Checklist of North American Birds* (AOU 1931), and two species again were recognized, *D. obscurus* and *D. fuliginosus*. These were interior ("Rocky Mountain") and coastal species rather than southern and northern Rocky Mountain species, as in the case of *D. obscurus* and *D. Richardsonii*. The fifth AOU *Checklist* (AOU 1957) returned *fuliginosus* to subspecific level, and *Dendragapus* was again a monotypic genus. The sixth *Checklist* (AOU 1983) merged spruce grouse, formerly in the genus *Canachites*, into *Dendragapus*, a result mainly of studies by Short (1967). This change was partly an attempt to reduce the number of monotypic genera within the Tetraoninae and was questioned (Boag and Schroeder 1992).

Spruce grouse were later removed from *Dendragapus* by the AOU (1997), again creating a monotypic genus (see 14.2.1). More recent DNA analyses suggest the dusky and sooty blue grouse groups may be separate species (Gutierrez et al. 2000), as first adopted in 1931 (AOU 1931), but this has not been formally recognized. There is now one recognized species, with eight subspecies.

(c) *Subspecies groups.* Subspecies may cause problems of identification. Nevertheless, three clear groups can be identified with even minimal experience. If one accepts the eight races noted above, they can be divided into an "interior", "dusky", or "*obscurus*" group which includes *D.o. obscurus*, *D.o. oreinus*, *D.o. pallidus*, and *D.o. richardsonii*, and a "coastal", "sooty", or "*fuliginosus*" group which includes *D.o. fuliginosus*, *D.o. sitkensis*, *D.o. sierrae*, and *D.o. howardi*. Characteristics that help distinguish these groups are as follows:

(1) Downy young grayish in interior birds; yellowish in coastal birds.
(2) General hue of interior females brownish gray; coastal females brownish to reddish brown.
(3) Lateral cervical apteria reddish and slightly tuburculate in interior males, underlaid with little dermal fat; yellow and strongly tuburculate in coastal males, underlaid with much dermal fat.
(4) Song of interior males very soft, usually inaudible beyond 100 m, and usually given from the ground; syrinx larger than in coastal males; song of coastal males often audible to at least 300 m, and, except where forests have been removed by logging or fire, usually given from trees.
(5) Song of interior males most often with five syllables, that of coastal males with six.
(6) Complex flutter flight in interior males, simpler flutter flight in coastal males. Flutter flights more frequent in interior birds.

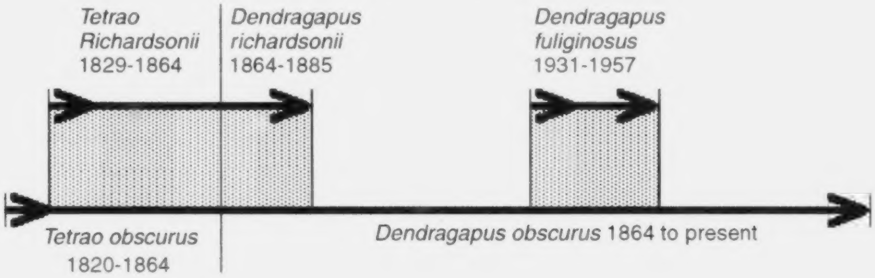

Tetrao Richardsonii 1829-1864
Dendragapus richardsonii 1864-1885
Dendragapus fuliginosus 1931-1957
Tetrao obscurus 1820-1864
Dendragapus obscurus 1864 to present

Fig. 4.1. Principal changes in the taxonomy of blue grouse at the levels of genus and species. Shaded areas represent periods when two species were recognized.

(7) Tail squarish and individual rectrices truncate in interior birds; tail and individual rectrices more rounded in coastal birds.

Within interior birds there is again a clear separation. Southern interior forms (*D.o. obscurus* and *D.o. oreinus*) have strong slate gray tail bands and usually 18 rectrices; northern forms (*D.o. pallidus* and *D.o. richardsonii*) have weak or no tail bands and usually 20 rectrices (Zwickel et al. 1991).

Objective criteria for separating coastal birds into two groups are not as clear. All have a clear slate gray tail band and a strong tendency to have 18 rectrices (Zwickel et al. 1991). There is, however, a gradient in width of the tail band—tending to decrease from south to north (see 8.1.3), and in general colouration—tending to darken from south to north. As well, there is a general habitat separation, with *D.o. sierrae* and *D.o. howardi*, found mainly in dry interior, or interior-like, habitats, while *D.o. fuliginosus* and *D.o. sitkensis* are largely confined to the more mesic western slopes of the central and north coast. Although physical criteria for separation are not as objective as for interior birds, there is a relatively sharp longitudinal habitat separation between them, but with extensive latitudinal overlap. The two southern and two northern groups of interior and coastal birds may be sufficiently distinct to be considered as four "supersubspecies".

4.2 Distribution

> *There are four main causes of limitation of range on land . . . The first three are climate, vegetation, and other animals; the fourth, physical barriers.*
>
> Wilma George (1962)

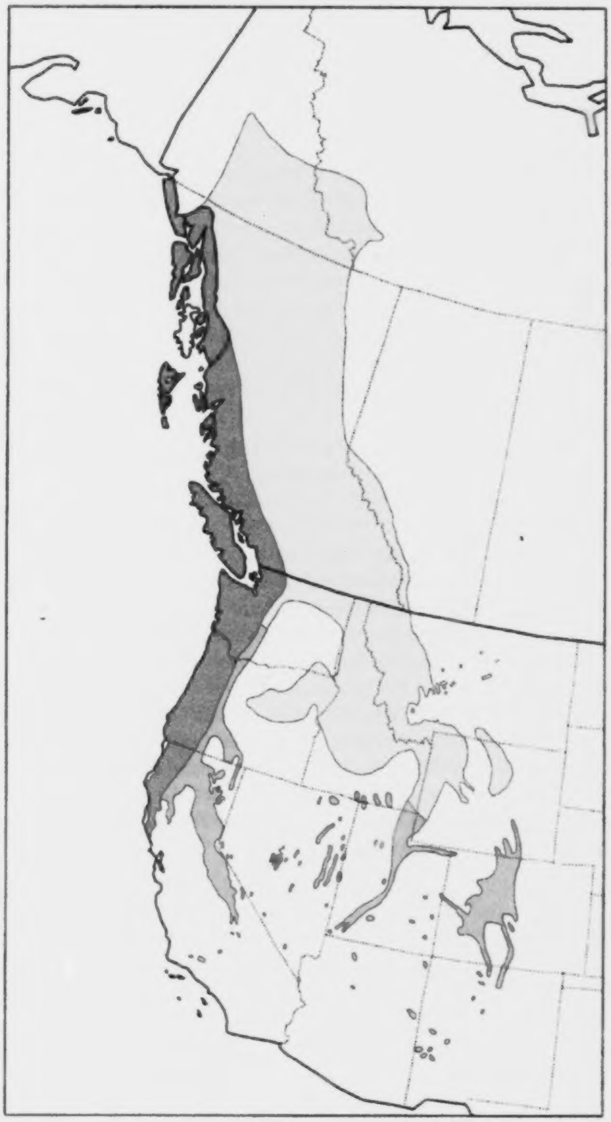
4.2.1 Continental distribution

Blue grouse are endemic to western North America and extend from the west coast, at sea level, to eastern slopes of the Rocky Mountains (Fig. 4.2), with their eastern most limit near Colorado Springs, CO. In general, interior races extend north and south along the Rocky Mountains and their outlier ranges, and coastal races north and south along the Sierra Nevada and Cascade and Coast Mountains, including their outlier ranges. The two groups coalesce in the northern Cascade Mountains, beginning at about the Kittitas Valley in Washington State. From there north, *D.o. pallidus* and *richardsonii* replace *sierrae* on the eastern slopes of these ranges. Precise boundaries between some subspecies are not well defined and may never be so because of continuous distributions and apparent subspecific hybridization, with gradients rather than sharp discontinuities in some morphological characteristics.

4.2.2 Subspecies and their distributions

The sixth and seventh editions of the *Checklist of North American Birds* (AOU 1983, 1998) do not list subspecies, but the fifth (AOU 1957) did. Eight races were recognized, four "interior" and four "coastal", and these are now generally accepted (e.g., Johnsgard 1983; Potapov 1985). We here note major features used to define them and their described areas of distribution:

Fig. 4.2. Distribution of blue grouse by subspecies pairs: green, *D.o. obscurus* and *oreinus*; orange, *D.o. pallidus* and *richardsonii*; pink, *D.o. howardi* and *sierrae*; blue, *D.o. fuliginosus* and *sitkensis*. See text for boundaries between subspecies within pairs.



(a) *Interior subspecies* (Dusky grouse group)

D.o. obscurus (Say), Dusky blue grouse—this, the nominate form, was described from a female from the Defile Creek area, ~30 km north of Colorado Springs, CO. Say gave a detailed description of the plumage, suggesting a likeness to the female black grouse, *Tetrao tetrix* (Say, in James, 1823) [tail band well defined].

Found on the northern rim of the Grand Canyon, in isolated pockets of northeast (Chuska Mts.) and eastcentral (White Mts.) Arizona and northwest and westcentral New Mexico, south to the Mogollon Rim, and in the northern Rocky Mts. of New Mexico; then northward in the Rocky Mts. of Colorado and Utah, including the Uintah and Wasatch mountains, and into southeastern and southwestern Wyoming and southeastern Idaho; likely intergrades with *D.o. pallidus* at about the level of Pocatello, ID, and perhaps with *D.o. oreinus* in southeastern Idaho and northwestern Utah. Precise boundaries of the three subspecies are unclear in this region. Reported on San Francisco Peak, AZ (Merriam 1890), but this is discounted by Brown (1972).

D.o. oreinus Behle and Selander, Great Basin blue grouse —similar to *D.o. obscurus* but more pale and with more white on the scapulars (male). Females more pale and more gray than *obscurus*. Most pale of all blue grouse. Differs from *D.o. pallidus* and *D.o. richardsonii* by having a distinct gray tail band (Behle and Selander 1951).

Occurs as small discontinuous populations in disjunct mountain ranges of the Great Basin in north and westcentral Utah, eastern and central Nevada, and perhaps into southeastern Idaho. Separated from *D.o. obscurus* by extensive shrub-steppe desert west of the Wasatch Mts. in Utah and from *D.o. sierrae* by extensive shrub-steppe desert east of the Sierra Nevada.

D.o. pallidus Swarth, Pallid blue grouse—most like *D.o. obscurus* in general colouration but without a well-defined gray tail band. Similar to *D.o. richardsonii* in the latter respect, but more pale (Swarth 1931). No other clear distinctions.

Inhabits the Rocky Mts. of western and northcentral Wyoming, western Montana, eastern and northern Idaho (except the southeastern corner where it may intergrade with *D.o. obscurus* and *D.o. oreinus*), northeastern and northcentral Washington[2] and northward in the central interior of British Columbia to about 52°N on east slopes of the Cascade and Coast mountains. Extends westward from westcentral Idaho into the Blue Mts. of southeastern Washington and northeastern Oregon and Wallowa Mts. of northeastern Oregon. Small discontinuous populations occupy disjunct mountain ranges of central Montana, eastward to at least the Judith Mts. and some breaks of the upper Missouri River.

D.o. richardsonii (Douglas), Richardson's blue grouse—described from birds on the east slopes of the Rocky Mts. in the present Province of Alberta. Douglas described the male mainly on the basis of plumage and provided a less detailed description of the female (Douglas 1829). Most like *D.o. pallidus*, but darker [tail band absent or poorly defined].

Occupies the Rocky Mts. of southwestern Alberta and southeastern British Columbia, northward in interior mountain ranges to southwestern Northwest Territories in the Liard and Mackenzie mountains and into southern Yukon Territory, extending to central Yukon in the southern Ogilvie Mts. (D Mossop, pers. comm.). Replaces *D.o. pallidus* northward on eastern slopes of the coast ranges from ~52°N. Northern boundaries poorly defined.

(b) *Coastal subspecies* (Sooty grouse group)

D.o. howardi Dickey and Van Rossem, Mount Pinos blue grouse—nearest to *D.o. sierrae* but more pale and with more conspicuous vermiculations (male). Tail of *D.o. howardi* longer, more graduated, and with a wider band (Dickey and Van Rossem 1923). No description of female.

Occurs in the Los Padres National Forest (especially Mt. Pinos and Frazier Mt.) and in the Tehachapi Range in southern California (but see 4.2.4), then northward in the Sierra Nevada of California and western Nevada to ~37°N. Boundary between *D.o. howardi* and *D.o. sierrae* not well defined.

D.o. sierrae Chapman, Sierra blue grouse—described as most like *D.o. obscurus*, with differences between the races leaning heavily on more black and brown vermiculations in *D.o. sierrae*. Differs from *D.o. fuliginosus* by being paler and more vermiculated. Females of the three races are difficult to separate, but those of *D.o. fuliginosus* may be less pale and perhaps more reddish (Chapman 1904). [All of these forms have gray tail bands, but those of the first two tend to be wider. In song, behaviour, and colour and texture of the lateral cervical apteria of males, *D.o. sierrae* and *D.o. fuliginosus* are most alike. Most biologists today would agree that the latter two are most similar.]

Inhabits the Sierra Nevada of California and Nevada, beginning at ~37°N; extends north along the Sierra Nevada and west in northcentral California to eastern slopes of the coast mountains, then north along eastern slopes of the Cascade Mts. in Oregon and Washington to about the Kittitas Valley, WA. Boundary with *D.o. pallidus* poorly defined. Outlier populations exist in the White Mts. of eastcentral California and westcentral Nevada and in the Warner Mts. of northeastern California and southcentral Oregon.

D.o. fuliginosus (Ridgway), Sooty blue grouse—"Most nearly resembling var. *obscura* (as distinguished from var. *Richardsonii*), but the colours much darker in shade, and the dark areas more prevalent. In specimens from the Sitka district the upper parts much washed with castaneous-rusty" (Baird and Ridgway 1873, p. 199). [Ridgway apparently put heavy emphasis on the fact *D.o. obscurus* and *D.o. fuliginosus* both have distinct gray tail bands and a tendency toward 18 rectrices, while *D.o. richardsonii* has an indistinct, or no, tail band and a tendency toward 20 rectrices. In other ways, e.g., song, some behaviours, and colour and texture of the lateral cervical apteria of males, *obscurus* and *richardsonii* are most alike. Most biologists today would agree that the latter two are most closely related.]

An inhabitant of north coastal California, beginning in Sonoma County (Dawson 1923); extends northward along the Pacific slope to Prince Rupert, BC; early historical accounts indicate they occurred as far south as Napa (Coues 1874), and Bodega Bay (Grinnell and Whythe 1927), CA, but it is not clear whether they still occupy these areas. Mainland dividing line between this race and *D.o. sitkensis* is at about the Portland Canal just north of Prince Rupert, BC. Also occupies many coastal islands, including Vancouver Island, BC.

D.o. sitkensis Swarth, Sitkan blue grouse—described on the basis of the female. Most like *D.o. fuliginosus*, but much more reddish in virtually all parts of the plumage. Males of the two forms not distinguishable (Swarth 1921) [tail band well defined].

Southern boundary said to be Calvert Island, BC, ~110 km north of Vancouver Island. Extends north on coastal islands to the Queen Charlotte Islands, BC, and most of the major coastal islands of southeast Alaska (except Prince of Wales Island).[3] Inhabits all of mainland southeast Alaska to at least the Tanis Mesa area, ~65 km southeast of Yakutat (B Dinneford, pers. comm.). Dinneford cites unconfirmed reports in the Dangerous River area, ~30 km southeast of Yakutat. Extends north from Haines along the Haines Highway to upper timberline.

Some subspecific descriptions are based on few specimens, subjective criteria, and have not adequately documented the range of variation that occurs in nature. Even a taxonomist with complete descriptions at hand might have trouble in placing many individuals into a particular race without knowing from whence they came. Subspecific taxonomy should be reexamined, for all subspecies have common borders with at least one other race, some have been described only cursorily, and because of introgression, common boundaries of some races are poorly defined.

4.2.3 Island populations

Blue grouse inhabit many coastal islands. Although we have not made detailed analyses of insular distributions, it is our impression that islands more than ~2 km from a source population are usually uninhabited (unless introduced by humans). Thus, 2 km may be about the limit of sustained level flight of this species. Some coastal islands may have been colonized during glacial periods when interisland channels were narrower (or absent) than at present, a result of lower sea levels along parts of the inner coasts of British Columbia and Alaska (Clague 1981). Recent evidence indicates some islands were connected to unglaciated coastal plains on the mainland by land bridges toward the end of the last glacial period (Anonymous 1991), providing possible routes for colonization.

A major exception to the above generalization is the occupation of the Queen Charlotte Islands, BC, ~100 km from any other land. Taverner (1940) implied that blue grouse flew there, but we doubt this. If not, one can only speculate on how they may have arrived for there are no historical records of introduction by humans. Hecate Strait, between the Queen Charlottes and the mainland, is shallow, and the present sea bottom was a vegetated and unglaciated land bridge that connected the islands to the mainland as recent as 13 000 years BP (Koppel 1996). Although virtually all of British Columbia was covered by ice during the Pleistocene (Clague 1981), there may have been unglaciated coastal plains (Anonymous 1991). A land bridge from the mainland seems the most likely explanation for the presence of blue grouse there. A second possibility is that grouse colonized the Queen Charlottes in an earlier nonglacial interval and survived Wisconsinan glaciation in a refugium, for the ice cover may not have been as extensive as on the mainland (Clague 1981). This leaves the question unanswered as to how they first arrived, however.

Local and disjunct populations of blue grouse also occupy many isolated mountain ranges, "islands" of habitat, removed from more continuous areas of distribution. If far removed from other populations, they may have colonized these areas when different plant communities prevailed and which may have been continuous with the major cordilleras. In this context, these populations represent post-glacial relicts. An alternative explanation is that grouse may have crossed dry non-forested valleys along moist riparian corridors (Johnson 1975). Within their areas of distribution (Fig. 4.1) there also are "islands" of "non-habitat" in which blue grouse do not occur, e.g., extensive alpine tundra or extensive closed canopy forest, but that cannot be delineated here because of inadequate information and the scale of our work.

4.2.4 Extirpations from historic range

With few exceptions, there have been no major extirpations from historic range. One possibility involves *D.o. howardi* in the southern end of its distribution in the Mt. Pinos and Tehachapi Mt. regions. Blue grouse were considered extremely rare in the Tehachapi, Mt. Pinos, and Frazier Mt. areas in the 1950s (AOU 1957), 1960s, and 1970s, with only sporadic sightings reported. Janet Hamber (1976), and two colleagues observed a blue grouse on Mt. Abel on 23 September 1976, and BT Harbour (letter, 9 October 1978) and Mike LeFevre saw an adult male on 2 June 1978 on Frazier Mountain. Harbour noted, "It is believed to be the only reliable observation in several years . . ." Lentz (1993) reported three sightings by others in the early 1990s, one each in 1991, 1992, and 1993, of which the latter seems especially credible. A few grouse may still exist in the Mt. Pinos and Frazier Mt. areas, but these populations are, if not gone, in danger of extirpation (Bland 1997, 2003). Other local extirpations have occurred in areas of agricultural, industrial, and urban development, e.g., in the Portland, OR, area (Jewett and Gabrielson 1929) and in lowlands in the Puget Sound trough, WA (pers. observ.).

One likely error in reporting of the historic range has occurred. The fifth, sixth, and seventh editions of the *Check-list of North American Birds* (AOU 1957, 1983, 1998) record this bird as resident in western South Dakota ("formerly" so in the sixth edition, p. 137). GB Grinnell reported seeing a blue grouse in the Black Hills of Wyoming during an expedition to this and the Black Hills of South Dakota (Ludlow 1875). Four specimens reported as collected in the Black Hills of Nebraska in 1856 and 1857 (Baird 1858) were obtained by a Lt. Bryan, whose expedition was to the Missouri Valley and the upper Platte River. These specimens (one now at the Smithsonian Institution) most likely were obtained in the Laramie Mts. in Wyoming, which were, at the time, part of Nebraska Territory and also referred to as the Black Hills. In our examination of over 2300 museum specimens in collections from across North America, none was reported to have come from South Dakota. As well, blue grouse are not recorded as an indigenous species in Natural History of the Black Hills (Froiland 1978). It is doubtful they occurred there naturally (L Rice, pers. comm., 29 July 1986), the only suitable habitat for them in South Dakota.

4.2.5 Introductions into unoccupied range

At least six attempts have been made to introduce blue grouse into areas outside their natural range and seven to establish them on previously uninhabited Islands within this range (Table 4.2). A brief history of these introductions follows:

Ontario — this was the only attempt to establish the species outside of western North America. Twenty-one birds were captured at Beavertail Lake on Vancouver Island and released in Sibley Provincial Park, near Thunder Bay. The introduction was not successful (Speirs 1985).

New Mexico — from 1961 to 1963, 56 grouse were trapped north of Chama, NM and released in the Bear Canyon area of the White Mts.; four had been released in the White Mts. in 1960. The release site was ~160 km from the nearest known

Table 4.2. Introductions of blue grouse into unoccupied range.

No. of birds							
Adult[a]		Juvenile				Current	
Male	Female		Date	Origin	Release site	status[b]	Source(s)[c]
					ONTARIO		
0	5	16	August 1955	Beavertail Lake, BC	Sibley Prov. Park	X	5, 9
					NEW MEXICO		
0	1	3	1960	Chama, NM	White Mts.	?	8
0	1	8	1961	Chama, NM	White Mts.	?	8
0	7	29	August 1962	Chama, NM	White Mts.	?	8
0	4	7	August 1963	Chama, NM	White Mts.	?	8
0	3	8	August 1969	Chama, NM	Mt. Taylor	E	6
					ALASKA		
0	17	12	1962–1964	Mitkof Island, AK	Kodiak Island[d]	X	4, 12
					SOUTH DAKOTA		
1	10	11	July 1969	Craig, CO	Black Hills	X	7
0	2	8	August 1974	Craig, CO	Black Hills	X	7
					BRITISH COLUMBIA		
135[e]			1944–1947	Vancouver Island, BC	Texada Island	E	10
20	20	0	May 1970	Vancouver Island, BC	Sidney Island	X	2
20	20	0	May–June 1970	Vancouver Island, BC	Portland Island	X	2
60	60	0	May–June 1970	Vancouver Island, BC	Moresby Island[f]	E	2
12	11	0	July 1971	Vancouver Island, BC	Lasqueti Island	E	1
					WASHINGTON STATE		
20	20	0	May 1970	Vancouver Island, BC	Stuart Island	X	2
15	8	0	May 1973	Vancouver Island, BC	Orcas Island	X	11
					ARIZONA		
0	1	4	August 1975	White Mts., AZ	San Francisco Peaks	E	3
0	5	15	July–August 1976	White Mts., AZ	San Francisco Peaks	E	3

[a] Adult presumably includes yearlings, which often is not specified.

[b] E, apparently established; X, apparently failed; ?, unknown.

[c] 1, BC Fish and Wildlife Branch; 2, Bergerud and Hemus (1975); 3, Brown (1977); 4, Burris and McKnight (1973); 5, J Hatter (letter, 22 Nov. 1955); 6, J Herring (letter, 2 April 1986); 7, Kranz (1976); 8, Merrill (1967); 9, Speirs (1985); 10, Sugden and Mitchell (1951); 11, Washington Dept. of Game; 12, Weeden (1965).

[d] 30 birds released; sexes and ages available for only 29.

[e] 32, 33, 33, and 37 birds each year, respectively. Sexes and ages unknown.

[f] Moresby Island in the Gulf of Georgia; there is a second Moresby Island in the Queen Charlotte Islands, BC.

population. In 1969, 11 were trapped near Chama and released in the La Mosca Peak area of Mt. Taylor. Bailey (1928, p. 198) shows this as previously occupied range but noted that according to Ligon (1926; cited in Bailey, not seen by us), "none now remain . . . on top of Mount Taylor". This site, in 1969, was ~100 km from the nearest population. If any grouse remain in the White Mts. they are very scarce, and there is a remnant, but sparse, population on Mt. Taylor (J Herring, letter, 2 April 1986). The White Mts. were outside historic range, but had been determined as potentially suitable habitat.

Alaska — eight grouse from near Petersburg, AK, were released on the Chiniak Peninsula, Kodiak Island in 1962, one in 1963. In 1964, 21 were released on Spruce Cape, Kodiak Island (Weeden 1965). These introductions appear to have failed (Burris and McKnight 1973). Kodiak Island is ~800 km south and west of the western most distribution of blue grouse.

South Dakota — as noted above, there is doubt as to whether blue grouse were indigenous in South Dakota and northeastern Wyoming—we consider it unlikely. Birds for two introductions (1969 and 1974) were captured near Craig, CO. The release sites, Fox Creek Campground (1969) and Harney Peak (1974), were ~200 km from the nearest known population, in the Laramie Mts., WY. One sighting and one recovery (1971) resulted from the 1969 release and none from 1974. These introductions are considered unsuccessful.

British Columbia — virtually all of British Columbia is within the range of blue grouse, but some offshore Islands are unoccupied. From 1944 to 1947, the BC Wildlife Branch introduced grouse on Texada Island, in four lots, one each year. All were released near Northeast Point and Pocahontas Bay. By 1951 they were established in virtually all parts of the Island, at low densities (Sugden and Mitchell 1951). In 1987 small numbers were still present throughout the island (R Forbes, pers. comm., 12 January 1987).

In 1970 Bergerud and Hemus (1975) conducted experimental introductions of blue grouse from Vancouver Island onto three islands in the Gulf of Georgia and nearby Stuart Island in Washington State. Forty birds from each of Comox Burn and Copper Canyon were released on Sidney (932 ha) and Portland (195 ha) islands, respectively. Forty from near Middle Quinsam were released on Stuart Island (556 ha). Twenty of each stock were released on Moresby Island (599 ha). The Sidney introduction failed early, even though anecdotal reports indicate blue grouse once lived there. Birds released on Portland and Stuart islands were present to at least 1977 (Bergerud 1988). Both populations now appear to have been extirpated, that on Portland perhaps because of low juvenile survival, and that on Stuart perhaps related to poaching (AT Bergerud, pers. comm.). Personnel of the Washington Dept. of Game searched for but neither saw nor heard grouse on Stuart from 1981 to 1985; nor were any seen by island residents (CF Martinsen, letter, 3 April 1986). Birds there are presumed extirpated.

In 1971, local residents introduced grouse from Mt. Washington, Vancouver Island, to Lasqueti Island in the Strait of Georgia. As of 1986, birds were distributed throughout the island, at low density (E Darwin, pers. comm. 19 November 1986).

Washington State — in spring 1973, grouse from the Mt. Washington area, Vancouver Island, were released on Orcas Island in the San Juan archipelago. Several were seen that autumn, and males were heard singing in spring 1974. A leg from an original bird (all were banded), and legs of unbanded juveniles were found in autumn, apparently from poached birds. Unbanded birds indicate successful breeding in 1974. No grouse were seen or heard by personnel of the Dept. of Game or residents of the island from 1981 to 1985, and they are presumed extirpated (CF Martinsen, letter, 3 April 1986). See above, British Columbia, for information on an introduction to Stuart Island, WA.

Arizona — grouse were released into the San Francisco Peaks in 1975 and 1976; again, there is some doubt as to whether blue grouse had been indigenous to the area. All birds were banded and unbanded birds were recovered, indicating successful reproduction. In 1986, the area was opened to hunting (DE Brown, letter, 7 April 1986). The release site was ~75–80 km from the nearest known population, on the north rim of the Grand Canyon.

Blue grouse now have been released at 13 previously unoccupied sites. In only five are they considered established. Two successful introductions were at mainland sites, Mt. Taylor, NM, and San Francisco Peaks, AZ (among five attempts), and three onto Islands, Texada, Moresby, and Lasqueti islands, BC (among eight attempts). Populations persisted for a few years on Portland and Stuart islands, but eventually died out.

Only in the case of island populations studied by Bergerud and Hemus (1975) were post-introduction densities well documented, and all were relatively low in comparison to nearby populations on Vancouver Island. Small populations may be especially vulnerable to stochastic extrinsic factors such as poaching, which has been implicated as a potential cause of failures on Stuart and Orcas islands. Some islands may have been too small (all except Texada, Lasqueti, Orcas, and Kodiak were <10 km^2), or had too little suitable habitat to maintain viable populations over extended periods of time.

In the case of mainland introductions, two were clear failures (Ontario and the Black Hills), and both were almost certainly well outside the native range of blue grouse. The release in Ontario may have been complicated because coastal birds were released into an interior habitat. Among other mainland introductions, that onto Mt. Taylor was within the former range of the species, the other two a short way from native range. The only mainland introduction considered to be clearly successful was onto San Francisco Peaks. Other areas may have had only marginal habitat, for densities appear to be very low, or perhaps extirpated (White Mts., NM). Attempts to introduce this bird into new areas have met with only limited success.

4.3 Synthesis

Although Lewis and Clark provided the first written descriptions of blue grouse (6.2.2; Zwickel and Schroeder 2003), some aboriginal groups separated them from other tetraonines by specific names, almost certainly before the arrival of Europeans in North America. Early explorers and naturalists often used different vernacular names for this bird, but "blue grouse" eventually prevailed.

The scientific nomenclature for this species has gone through numerous changes since it was first specifically named (1823), and at times it was separated into two species. At present it is considered monotypic, *D. obscurus*, with eight subspecies that are divided into two groups, one interior and one coastal (each with four subspecies). As a result of recent DNA studies, Gutierrez et al. (2000) have proposed that interior and coastal birds should be considered separate species, *D. obscurus* and *D. fuliginosus*, as earlier recognized. The taxonomic status of this bird is still in a state of flux, and with more refined techniques and studies, we expect changes.

Blue grouse occupy most major mountain ranges of western North America. From east to west they range from eastern slopes of the Rocky Mountains to sea level on the Pacific Coast. From south to north, they range from New Mexico, Arizona, and southern California to southeast Alaska, the Yukon, and the Northwest Territories. Most of their original range is still occupied, with principal exceptions being intensely farmed or highly urbanized and industrialized regions. Attempts to introduce them into unoccupied areas have met with only limited success.

Endnotes [Chapter 4]

1. Feathers extend along the entire length of the toes in ptarmigan (*Lagopus* spp.), with no pectinations.

2. Once thought to meet *D.o. sierrae* on eastern slopes of the Cascade Mountains at about the level of the Wenatchee Valley (Jewett et al. 1953; Aldrich and Duvall 1955), but recent observations suggest the Kittitas Valley is a more likely boundary (pers. observ.).

3. We have noted a difference in the song of males on the Queen Charlotte Islands (similar to that of males on Vancouver Island and other coastal areas to the south) and that of males on Admiralty, Douglas, and Mitkof islands, and in the Skagway and Chilkat Pass areas of Alaska. In the latter areas the song appears louder and has a more hollow sound, as if the bird were singing from inside a barrel. If this reflects a taxonomic difference, birds now assigned to *D.o. sitkensis* in the Queen Charlotte Islands and south to Calvert Island may be more closely related to *D.o. fuliginosus* than to *D.o. sitkensis*.

CHAPTER 5

Evolution

Separation of a species into groups of individuals takes place incessantly, and in such groups mutations can be established and spread.

Sherwin Carlquist (1965)

Evolutionary relationships can be viewed at different levels. We examine the fossil record for *Dendragapus*,[1] phylogenetic relationships of blue grouse to presumed near relatives, and the possible derivation of extant subspecies.

5.1 The fossil record

Fossils of *Dendragapus* are uncommon. Three species later assigned to this genus were first described by Shufeldt (1892) from late Pleistocene deposits at Fossil Lake, OR. Shufeldt placed two, *D. lucasi* and *D. nanus*, in the genus *Pedioecetes* and one, *D. gilli*, in *Palaeotetrix*, a new genus. Howard (1946), however, pointed out that *D. lucasi* and *D. nanus* were really species of *Dendragapus*, and Jehl (1969) combined them as *D. lucasi*. Earlier, Jehl (1967) had noted that *Palaeotetrix* was not distinguishable from *Dendragapus* and suggested its elimination. These changes reduced the number of fossil species to two, *D. lucasi* and *D. gilli*.

The narrow series of beds from which these fossils were taken are not more than 29 000 years old [late Pleistocene] according to Allison (1966); Brodkorb (1964) considered them Middle Pleistocene. Among remains found there, *D. lucasi* was relatively common (Howard 1946), but *D. gilli gilli* [see below for a separation into two subspecies] is still known from only two carpometacarpi (Jehl 1969). *D. lucasi* is distinguished from *D. obscurus* by its small size and minor characteristics of the tarsometatarsus. *D. gilli gilli* was larger and more robust than *D. obscurus* or *D. lucasi*.

Miller (1911) reported that fossil remains of *D. obscurus* were numerous (>114 specimens) in the Samwel and Potter Creek caves in Shasta County, CA. Age of these specimens is considered late Pleistocene (Jehl 1969). Jehl concluded that they represent a small race of extinct *D. gilli*, to which he assigned the subspecific name *milleri*. He summarized the fossil evidence for early *Dendragapus* as representing two species, *D. lucasi* and *D. gilli*, the latter including two races, *D.g. gilli* and *D.g. milleri*. He suggested that the exact relationship between these species and *D. obscurus* is unclear but that *D. lucasi* is the most likely ancestor of *D. obscurus*.[2]

Remains of *D. obscurus* were found in an Indian midden in the Puget Sound, WA, region (Miller 1960) and in the Weiss[3] and Birch Creek Valley rock shelters in Idaho (Miller 1963). Carbon 14 dating indicated a maximum age of 10 000–12 000 years BP for the Idaho remains (Jehl 1969). See also 6.1.

5.2 Phylogeny and extant tetraonines

5.2.1 Phylogenetic trees

Several authors have constructed phylogenetic trees to explain evolutionary relationships among extant tetraonines (Clark 1899 and Wing 1946 considered North American genera only; Short 1967, Fjeldsa 1977, Johnsgard 1983, and Potapov 1985 considered all species). Criteria used to erect these dendrograms vary from only one, e.g., Clark, to several, e.g., Short. Although specifics vary, Short, Fjeldsa, and Johnsgard suggested that *Tympanuchus* was the first offshoot from a pre-extant tetraonine ancestor. Potapov suggested *Bonasa* first diverged from the main line, then *Tympanuchus*. Dendrograms by Short, Johnsgard, and Potapov are similar overall, differing mostly in detail and that of Fjeldsa is the most divergent. Short and Johnsgard suggested a North American origin for the tetraonines, Potapov, a Eurasian origin. Fjeldsa thought a snowcock (*Tetraogallus* sp.) or Monal partridge (*Tetraophasis* sp.)-like phasianid was their progenitor, implying an Asiatic origin. His dendrogram was based on downy plumages only, but he said it is supported by a cladistic analysis of anatomical characters. We think available evidence best supports Fjeldsa's phylogeny [except his suggestion of an Asiatic origin—recent molecular evidence suggests a Nearctic origin for the grouse (Lucchini et al 2001; Drovetski 2003)]. This is not the place, however, to try to sort out the entire history of the tetraonines. Here, we examine possible roots leading to blue grouse and this bird's relationship to its presumed nearest relatives.

5.2.2 Recent taxonomic changes

Grouse are usually grouped into three broad types based on habitat: *prairie*, *forest* (or *woodland*), and *alpine*, with blue grouse classified as a forest species. Short (1967) moved the spruce grouse and sharp-winged grouse (*Falcipennis falcipennis*) into *Dendragapus*, a change adopted by the American Ornithologists' Union (AOU 1983). Potapov (1985) retained *Dendragapus* for two species of blue grouse (*D. obscurus* and *D. fuliginosus*) and placed the sharp-winged grouse and spruce grouse in *Falcipennis* (adopted by the AOU in 1997). He, Fjeldsa, Johnsgard, and Short all recognized close affinities between blue and sage-grouse (recently split into two species, *C. urophasianus* and *C. minimus* (AOU 2000)). Fjeldsa and

Potapov depicted blue grouse closer to sage-grouse than to spruce grouse in their dendrograms, while Short and Johnsgard placed them closer to spruce grouse. Are blue grouse most closely related to spruce or sage-grouse?

5.2.3 Closest relatives

A number of criteria are potentially useful, or have been used, to examine the relationships of blue grouse to other tetraonines. Relative to spruce and sage-grouse, these include the following:

(a) *Fossil record.* All blue grouse fossils are presumably late, or Middle, Pleistocene, providing little evidence of evolutionary history. Nevertheless, some fossils assigned to *Dendragapus* were first classified as *Pedioecetes* (see 5.1), suggesting possible affinities with that genus [now *Tympanuchus*], a grassland–woodland edge inhabitant. Howard (1946) concluded that tarsometatarsi of *D. lucasi* represent a blending of characters found in *Dendragapus* and *Centrocercus.*

(b) *Osteology.* Jehl (1969) noted that few characters are available that will distinguish bones of *D. obscurus* from those of *Pedioecetes*, *Tympanuchus*, and *Centrocercus.* To the best of our knowledge, there has been no clear effort to examine phylogenetic relations among extant grouse based on skeletal materials beyond that statement.

(c) *Sexual size dimorphism.* Sage-grouse show very strong sexual dimorphism in terms of body mass, with that of females ~50% that of males, about the same as in capercaillie. Blue grouse also show strong sexual dimorphism in body mass, females varying from ~65% to 80% as heavy as males, depending on season (see 9.1.1). In autumn, their mass dimorphism is similar to that of black grouse (*Tetrao tetrix*, females ~75% that of males (Zwickel et al. 1966)). Mass dimorphism of spruce grouse is small, females ~93% as heavy as males in autumn (Zwickel and Brigham 1974), and heavier than males at peak mass in spring (Boag and Schroeder 1992). They are more similar to rock (*Lagopus mutus*; Holder and Montgomerie 1993) and white-tailed (*Lagopus leucurus*) ptarmigan in this respect (Braun et al. 1993).

(d) *Plumage.* Fjeldsa (1977) suggested that natal plumages likely have not been subjected to heavy selection, implying they are a conservative character. Judging from his dendrogram, blue grouse are more closely related to sage-grouse than to spruce grouse. We, too, believe natal plumage of blue grouse is more similar to that of sage-grouse than to spruce grouse, which more closely approaches that of the ptarmigan. Short (1967) noted that natal plumage of blue grouse is quite different from that of spruce grouse, but concluded it is derivable from it. In contrast, he suggested juvenal plumages of blue and spruce grouse are very similar but did not compare that of blue to other grouse. He also indicated that relative size and shape of wings and tails are similar in spruce and blue grouse but, again, made no comparisons to other grouse. Shapes of tails of blue and spruce grouse are more similar than those of blue and sage-grouse. All three species show strong sexual dimorphism in adult plumages.

Numbers of rectrices vary within and among the different grouse, and Short (1967, p. 33) suggested this character ". . . is too variable to be taxonomically useful at the generic level." Each species, however, has strong modal numbers, suggesting they may have significance. Blue grouse clearly separate into two geographic groups in terms of modal numbers of rectrices, 18 or 20 (see 8.1.3). The only other genus with such variation is *Centrocercus*, also most typically with 18 or 20, although their variation tends to be bimodal within populations (Zwickel et al. 1991). Spruce grouse, along with all ptarmigan, typically have 16.

(e) *Cervical and supercilliary apteria.* Male blue grouse are the only "forest" grouse with highly specialized lateral cervical apteria that are exposed during courtship.[4] This character is held in common with sage-grouse, sharp-tailed grouse, and prairie-chickens (*Tympanuchus cupido* and *T. pallidicinctus*). Wing (1946) suggested that these specialized apteria of blue grouse are being lost, but observations of histological specimens by MA Degner (pers. comm.) indicate they are highly developed. They also are most strongly tuberculate of all species, and are large in relation to size of the bird.

The supercilliary apteria, or eye combs, are relatively large and strongly erectile during display in male spruce and blue grouse, but reduced and less erectile in sage-grouse (Hjorth 1970). They are yellow in blue grouse, except at peak display (transitory red; Hjorth 1970; Stirling and Bendell 1970), yellowish green (Hollett et al. 1984) or yellow (Johnsgard 1983) in sage-grouse, and red in spruce grouse (Boag and Schroeder 1992).

(f) *Myology.* Hudson et al. (1966) studied the appendicular musculature of various gallinaceous birds. They concluded that, among North American grouse, *Lagopus*, *Bonasa*, and *Canachites* are a closely related subgroup, *Pedioecetes* and *Tympanuchus* are another, and (p. 13) "*Dendragapus* appears closest to *Canachites* and *Centrocercus.*" Because *Canachites* is in a subgroup that excludes *Dendragapus*, one might suggest blue grouse are more like sage-grouse than spruce grouse on the basis of their work.

(g) *Syringeal and esophageal morphology.* Male spruce grouse are near mute during courtship (Boag and Schroeder 1992; pers. observ.), while male blue and sage-grouse are very vocal. Syringes of male spruce grouse show little modification beyond that of a simple tube, but those of blue and sage-grouse are clearly enlarged and structurally complex. That of blue grouse is largest and, in terms of shape, appears most complex among the three species (pers. observ.).

The anterior section of the esophagus (the *pars cervicalis*) of male blue grouse (Degner 1988) and sage-grouse (Honess and Allred 1942; Clarke et al. 1942) is expandable. Its inflation is thought to be largely responsible for swelling of the neck region during courtship, and to be associated with exposure of the lateral cervical apteria during display. When inflated, it may act as a resonating chamber for sounds produced in the syrinx (Degner 1988). This characteristic is absent in male spruce grouse (MA Degner, pers. comm.).

(h) *Mating system and courtship behaviour.* In terms of some aspects of breeding behaviour, blue grouse appear more like spruce than sage-grouse (Wing 1946). Male blue and spruce grouse occupy dispersed territories and perform courtship flights; sage-grouse are a lek species and have no courtship flights (Hjorth 1970). Blue and sage-grouse, however, have specialized anatomical features used in display (see (g) above) and not found in spruce grouse, and are much more vocal during courtship. Lumsden (1968, p. 89) noted "many elements" of the voice of sage-grouse and some aspects of display behaviour are similar to some of those of blue grouse.

(i) Egg colour and length of incubation period. Short (1967) summarized information on egg colour for the different genera of grouse. Except for size, he suggested eggs of *Canachites*, *Dendragapus*, and the paler eggs of *Centrocercus* are similar. In our view, background colour of eggs of blue and spruce grouse are most alike, but in terms of extent and kind of marking, those of blue and sage-grouse are most similar. Eggs of blue and sage-grouse are more lightly speckled and less splotched than those of spruce grouse, which more closely resemble those of ptarmigan.

Length of the incubation period averages 26 days in blue grouse (McKinnon and Zwickel 1988) and sage-grouse (Pyrah 1963). That of spruce grouse is ~23 days (Naylor 1988; Boag and Schroeder 1992).

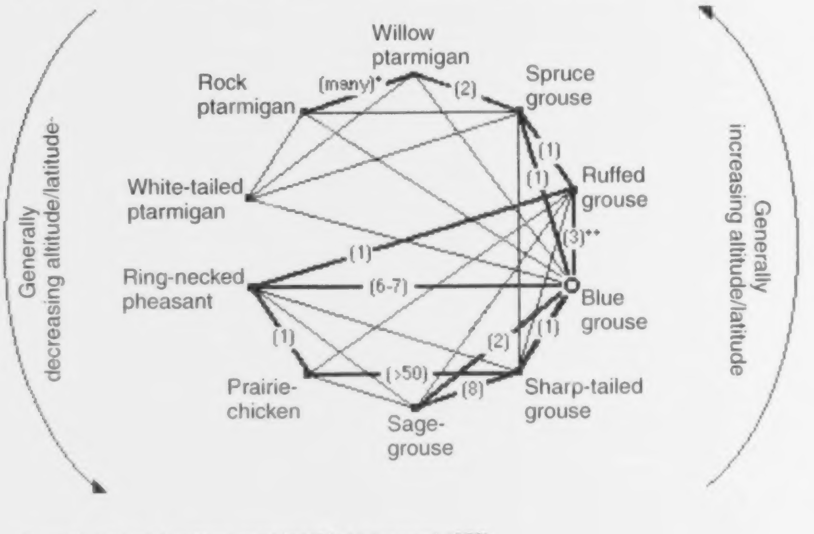
(j) Hybridization. Hybrids between blue grouse and other tetraonines, and with the ring-necked pheasant (*Phasianus colchicus*), have been reported. Because intergeneric hybrids are so common among tetraonines (Johnsgard 1982), and sometimes occur between grouse and phasianines (Phasianini), their taxonomic significance is difficult to evaluate. They suggest, at least, a relatively close relationship among tetraonines and phasianines. Within North America, more kinds of hybrids between blue grouse and other species have been reported than for any other grouse (Fig. 5.1). This may reflect in part the broad range of habitats occupied by this species in spring and summer, an attribute that brings them into breeding season contact somewhere with all North American species except the prairie-chickens.

(k) Habitat and food habits. Blue grouse occupy a great variety of habitats in breeding season (Chap. 16), overlapping with spruce and sage-grouse. Those occupied in winter, conifer forest, and winter foods, conifer needles, are clearly most like those of spruce grouse.

(l) Molecular genetics. Recent studies of mitochondrial DNA indicate spruce and blue grouse are ". . . among the most genetically divergent tetraonine taxa in North America . . . these two species do not constitute a monophyletic lineage" (Ellsworth et al. 1995, p. 497). Later work by Ellsworth et al. (1996), Gutierrez et al. (2000), Lucchini et al. (2001), and Drovetski (2003) are consistent with this conclusion. See 14.2 for more detail from these studies.

In summary, blue grouse appear more like spruce than sage-grouse with respect to background egg colour, mating system and some aspects of mating behaviour, size and erectility of superciliary apteria, shape of tail, winter habitat, and winter foods. With respect to juvenal plumages, yearling and adult plumage dimorphism, hybridization, and breeding habitat, they do not clearly approach one or the other species most closely, or information is too limited on which to base a decision. In other characteristics, the majority, they appear most like sage-grouse. We think characters held most in common with spruce grouse, e.g., a dispersed polygynous mating system, courtship flights, background egg colour, winter habitat, and winter foods, could easily be derived through convergent sexual or natural selection. Some characters held most in common with sage-grouse appear more conservative, e.g., natal plumage, and most morphological attributes. Recent DNA analyses likely provide the strongest evidence for a closer affinity to sage-grouse than to spruce grouse.

Fig. 5.1. Hybridization among North American Tetraoninae and with the ring-necked pheasant. Heavy lines indicate reported hybridization, thin lines, breeding season sympatry without known hybridization. Figures in parentheses indicate number of reported hybrids. Except where noted, all records are from wild birds.



* Eurasia only, and perhaps questionable (Johnsgard 1973)

** In captivity only

We believe blue grouse likely evolved from an early prairie and (or) woodland edge adapted progenitor, probably in a southern continental environment, most likely in the southern Rocky Mountain area; the other stem leading to *Centrocercus*, or perhaps *Tympanuchus* (Gutierrez et al. 2000). If true, the movement by blue grouse into forest was a secondary adaptation, principally for use as winter habitat, an adaptation that has became virtually obligatory. Breeding in forested areas would be a more recent attribute, and since those that breed there tend to use open, or openings within, forests supports this view. This suggestion is in accord with dendrograms of Fjeldsa (1977) and Potapov (1985) but not with those of Short (1967) and Johnsgard (1983). Lumsden (1968) also suggested blue and sage-grouse evolved from a common progenitor, but which he suggested was a forest dweller.

5.3 Derivation of extant subspecies

The eight extant subspecies of blue grouse are clearly divisible into three groups, southern interior (*D.o. obscurus* and *D.o. oreinus*), northern interior (*D.o. pallidus* and *D.o. richardsonii*), and coastal, that might each be considered as subgroups (perhaps supersubspecies; see 4.1.2(c)). Coastal birds too might be separated into two subgroups, southern coastal (*D.o. howardi* and *D.o. sierrae*) and northern coastal (*D.o. fuliginosus* and *D.o. sitkensis*), although physical criteria for doing so are less clear than for interior birds. North coastal birds are separable from all other groups by their use of mesic, humid habitats, but are morphologically and behaviourally similar to south coastal subspecies.

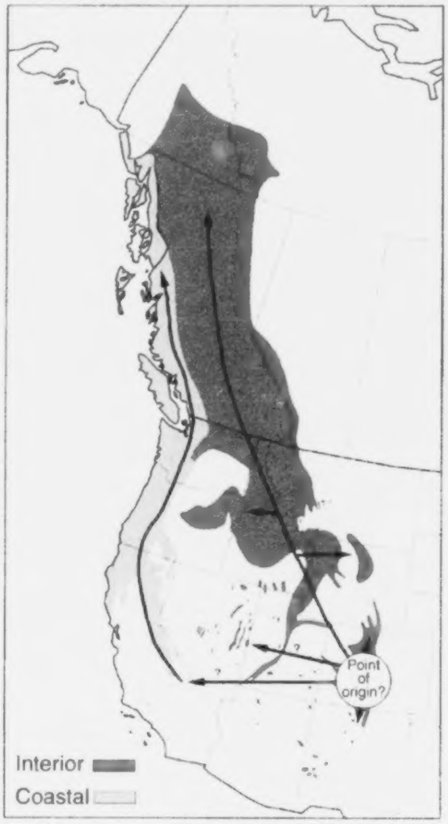
Southern interior birds are clearly most like northern interior birds in most respects, i.e., characteristics of song and flutter flights of males, lateral cervical apteria of males, size of male syringes, female plumage, and natal down. They are more like coastal birds in others, i.e., characteristics of tail bands and numbers of rectrices. Thus, in comparing interior and coastal groups, the southern forms within each appear more closely related to each other than do the northern interior and coastal forms. From this, one might build a case for a southern origin of blue grouse, with interior and coastal birds each expanding north, along the Rocky Mountains and the Sierra Nevada and Cascade–Coast mountain ranges, respectively, following the retreat of Pleistocene glaciation.

5.3.1 A possible scenario for the derivation of extant subspecies

Attempts to identify evolutionary pathways are always speculative. Nevertheless, we propose the following as a possible explanation for radiation and subspeciation in blue grouse:

(a) The scenario. We begin with a *Dendragapus* ancestor derived from a pre-blue grouse–sage-grouse or *Tympanuchus* ancestor somewhere in the southern Rocky Mountain region (Fig. 5.2). Ancestors of extant southern and northern interior birds may have been isolated from each other during a pre-Wisconsinan Pleistocene glaciation. Divergence within the interior group might have occurred in a fragmented refugium during, at latest, the Wisconsinan glacial interval, giving rise to progenitors of the *D.o. pallidus*–*D.o. richardsonii* and *D.o. obscurus*–*D.o. oreinus* subgroups, respectively. This would explain the tendency for *D.o. pallidus*–*D.o. richardsonii* to lose the tail band and to usually have 20, rather than 18, rectrices. Progenitors of coastal subspecies may have been isolated from those of southern interior birds at or before this time, initiating the development of three clear groups. South coastal subspecies, *D.o. howardi* and *D.o. sierrae*, appear well adapted to xeric, interior type forests, similar to those occupied by southern interior birds. They likely evolved from them. Possession of clear tail bands and a strong tendency to have 18 rectrices in *D.o. obscurus* (and perhaps *D.o. oreinus*) and all coastal subspecies also support an argument for the derivation of coastal birds from southern interior forms. If coastal birds were isolated from interior birds prior to Wisconsinan glaciation, progenitors of *D.o. fuliginosus* and *D.o. sitkensis* may have been fragmented from *D.o. howardi* and *D.o. sierrae* by glaciers along the spine of the Sierra Nevada, then have spread north along the Pacific slopes with the retreat of montane and coastal glaciers. The northern extent of *D.o. sitkensis* now appears limited by extant glaciers in southeast Alaska, and with continued deglaciation, these birds may expand to the north and west.

Fig. 5.2. Hypothetical evolutionary pathways of interior and coastal blue grouse from a centre of origin in the southern Rocky Mountain area.



With retreat of the most recent montane glaciers along the Rocky Mountains and Sierra Nevada and Cascade–Coast ranges, we envision that blue grouse were generally expanding northward, *D.o. obscurus* and *D.o. oreinus* coming to a halt when they met *D.o. pallidus*, with *pallidus* and *D.o. richardsonii* moving north in the Rocky Mountains, and west until they met *D.o. fuliginosus* at the crest of the Cascade–Coast Mountains. According to this scenario, *D.o. sierrae* would have been moving north along eastern slopes of the Cascade Mountains until they met *D.o. pallidus*. High desert developing in the Great Basin and southern Rocky Mountains was fragmenting occupied habitats at this time and isolating many populations on small mountain ranges, mainly *D.o. oreinus* in the Great Basin, some southern populations of *D.o. obscurus* in Utah, Colorado, New Mexico, and Arizona, and some populations of *D.o. pallidus* in the southern end of its range.

This scenario thus begins with *D.o. obscurus* and *D.o. oreinus* as closest to the stem group, and ends with *D.o. fuliginosus* and *D.o. sitkensis* as the most recent group. An attempt to depict the separation of subspecies within each pair is beyond our abilities at this time.

(b) *Paleobotanic evidence and the proposed colonization of coastal mountains by interior birds.* If blue grouse originated in the southern Rocky Mts. and dispersed westward to occupy coastal habitats, they would have had to cross the Great Basin, much of which is now unsuitable habitat. Evidence from palynological and packrat midden studies indicate that boreal evergreen conifers were widespread in this area 18 000 years BP, with woodland conifers in present southwestern deserts (Thompson and Anderson 2000). Other palynological evidence shows that forest and sagebrush communities during Wisconsinan glaciation were 900–1400 m lower than today in this area (Hall 1985). For example, vegetation at Tule Springs, NV (near Las Vegas), was dominated by sagebrush, with ponderosa pine parkland, then fir (*Abies* spp.), on nearby higher ground (since ~7000 years BP, Mohave Desert vegetation has occupied the valley bottom). Evidence from packrat middens also suggests southwestern forest communities occupied lower elevations than today—junipers (*Juniperus* spp.) and Douglas-fir grew ~760 m lower in the Grand Canyon 15 000 years BP (Friederici 2000). Other palynological data indicate Middle Pleistocene vegetation zones may have experienced shifts similar to those during Wisconsinin glaciation (Hall 1985). Such shifts would have provided plant communities through which grouse could disperse from the southern Rocky Mts. to the Sierra Nevada. Blue grouse [presumably *D.o. obscurus*] still occupy the Spring Mountains ~70 km northwest of Las Vegas (Stiver 1994), very near the California border.

There is some controversy as to whether intermountain valleys in the Great Basin were ever forested. Martin and Mehringer (1965) suggested they were, but Wells and Berger (1967) and Critchfield and Allenbaugh (1969) thought insular forest communities of today were established by long-distance dispersal of conifers across unforested intermountain valleys. It seems clear, however, that conifer dominated communities occupied lower elevations in the late Pleistocene (Hall 1985) and that valley bottoms as far south as Tule Springs were dominated by sagebrush. Johnson (1975, p. 558) suggested blue grouse "... probably could cross dry valleys without conifer forest if moist riparian strips were present . . ." Since some extant blue grouse populations occupy shrub-steppe in the breeding season (see 7.4.2), this is reasonable. In view of the insular distribution of montane conifer communities in the Great Basin today, and with such communities at even lower elevations in the late Pleistocene, or earlier, we believe blue grouse could have easily colonized the Sierra Nevada from the Rocky Mts., potentially at several different latitudes.

5.4 Synthesis

Fossils of *Dendragapus* are scarce and include two recognized pre-*D. obscurus* species, *D. lucasi* and *D. gilli*, likely from late Pleistocene deposits. Those of *obscurus* are all from archaeological excavations, dating back to 10 000–12 000 years BP. Owing to the scarcity of fossils for this genus, they provide little evidence for tracing its radiation from a point of origin. However, some palaeontologists have noted close affinities between these fossils and those of *Pedioecetes* (now *Tympanuchus*) and *Centrocercus*, suggesting a possible link to prairie grouse.

Both spruce and sage-grouse have been proposed as the nearest tetraonine relative of blue grouse. We believe most physical evidence supports an argument for placing sage-grouse closest to them, an argument supported by recent DNA studies. Blue grouse likely evolved from a common pre-blue-grouse–sage-grouse, or pre-blue-*Tympanuchus*, ancestor.

We suggest a possible scenario for the derivation of extant subspecies groups (pairs) of blue grouse. Our proposal rests heavily on the hypothesis that the species evolved from an open country progenitor and that radiation and subspeciation have resulted largely from advances and retreats of continental and (or) montane glaciers and of forest, shrub-steppe, and desert communities, advances and retreats caused by major climatic fluctuations.[5] We suspect this was taking place principally during Middle or late Pleistocene glaciations; consistent with the Pleistocene refuge hypothesis (Mayr 1963). Although speculative, we believe this sequence most closely approaches what is known from studies of extant subspecies and paleobotanic evidence. We find it difficult to accept that blue grouse evolved from a Eurasian (Fjelsda 1977; Potapov 1985) or pre-spruce grouse–blue grouse progenitor (Short 1967; Johnsgard 1983), or in a subalpine environment (Bergerud and Hemus 1975).

Endnotes [Chapter 5]

1. Excluding spruce grouse, formerly Canachites and now transferred into Falcipennis (AOU 1997).

2. Jehl (1969) considered *D.o. obscurus* closest to *lucasi* on the basis of similarity in robustness of *metacarpi* and *tarsometarsi*, both less robust than in *gilli*.

3. Blue grouse were the most prominent bird in the collection.

4. Short (1967) reported cervical "vocal sacs" in museum specimens of male spruce grouse, but this was disputed by Boag and Schroeder (1992), with whom we agree. All North American grouse of both sexes have lateral cervical apteria, but those of male spruce grouse show no signs of specialization or exposure during display.

5. Blue grouse have one of the smaller geographic ranges among the tetraonines but rank fourth in number of subspecies (Johnsgard 1983). The relatively large number of subspecies likely reflects the periodic fragmentation of populations by glacial and vegetation changes, combined with adaptations to the variable habitats in montane environments.

CHAPTER 6

Historical Review

You threw stones at me
The small grouse on the mountain [the wife]
From down in the valley.

From the Gitskan song, "Lodzahut",
translation by R Maud (1982)

6.1 Blue grouse and aboriginal peoples

North American Indians depended heavily on wildlife for food, tools, clothing, and cultural accoutrements. Grouse influenced northwest Indian art. They were featured in Kwakiutl masks and dances (Hawthorn 1979; Nolan 1988), and a grouse, part of a mythological story, is featured on a contemporary Gitskan totem pole at Kispiox, BC (Stewart 1990). "Lodzahut", a Gitskan song (see above), documents an incident in the marital life of Dzeeus, whose family crest was "Pistae'i", the blue grouse (Maud 1982).

This bird also figured in the mythology of other groups. Bella Coola Indians tell of interactions between Raven and Blue Grouse, Mo'xmuk^{u}t, in one such myth (Boas 1898). Bella Coola also believed blue grouse would give their infants the ability to sing, e.g.,

> "Boil together herbs and a bear's bladder and smear the decoction on the infant's back. He must thenceforth wear around his neck for several months a small sack containing four blue grouse gall-bladders . . . This gives the child the singing ability of the bird, . . ." (McIlwraith 1948, p. 703).

Clearly, blue grouse contributed to cultural lives of some aboriginal peoples.

Indians hunted blue grouse in many areas. For example, Townsend (1839), led by two Indian guides, hunted them in the Blue Mountains near present Walla Walla, WA, in July 1836. He wrote (p. 351), ". . . we saw large numbers of the dusky grouse (*Tetrao obscurus*), a number of which we killed. . . . We returned to our lodge in the evening loaded with grouse, . . ." JG Cooper (in Suckley 1860, p. 219) reported, ". . . in June flocks of half-grown young are murdered by the Indians near Puget Sound." In the Queen Charlotte Islands, Chittenden (1884, p. 35) described food habits of the Haida Gwaii, "Bear [*Ursus americanus*], wild geese [Anserini], duck [Anatinae], and grouse also contribute to their food supply, . . ." [blue grouse are the only grouse found there]. And Dawson and Bowles (1909, p. 578) noted, with reference to sooty grouse, "The Indians [of the Pacific Coast] used to be very skillful on the still hunt, especially in winter, . . ."

Robert Ridgway's first contact with this bird involved those he saw in the possession of Indians who had been hunting in the Sierra Nevada near Carson City, NV (Baird et al. 1874). A northwest-coast arrow (#A6754), fletched with rectrices of a female, is on display at the University of British Columbia Museum of Anthropology, and bags of rectrices, collected as Indian artifacts in Colorado, appear to have been intended for fletching arrows (Rogers 1968). In other areas, blue grouse may have been too scarce to attract much attention. For instance, Philips (1937) noted that they were sparse in the Chuska Mountains, AZ, and Navaho Indians there did not hunt them. Miller (1963, p. 179) found them to be ". . . the most prominent bird in the collection" from a Weiss Rock Shelter midden in westcentral Idaho. He also found them in a midden collection from the Birch Creek Valley Cave, north–northeast of Pocatello, ID (along with numerous bones of sage-grouse), but represented by only eight bones. These middens were considered borderline between Recent and Pleistocene, not more than 10 000–12 000 years BP.

In some northwest coastal areas, this grouse does not seem to have been especially important as food. For example, Miller (1960) examined some 500 avian bones or bone fragments that were collected from nine shell middens in the Puget Sound area and found only two of blue grouse (<1%). Remains of ducks, about the same size of bird, were abundant. An archaeological excavation on Vancouver Island netted one bone from blue grouse, although remains of water birds were common (Mitchell 1980). Blue grouse are common in this region today and should have been readily available to early residents. Few grouse artifacts from these regions may indicate they were less common at one time, or may reflect that local natives seldom strayed far from the sea.

6.2 Early explorers and naturalists

Western North America was settled by those of European descent much later than eastern portions of the continent. Early expeditions to the west came relatively late, and the period of exploration was short as the area was rapidly occupied. Nevertheless, much of the stimulation for exploring the west was to evaluate its resource potential, and plants and animals were of major concern. In other cases natural history was not a significant concern, and botanical and faunal records were limited to plants and animals taken for food or of concern as predators. There was a tendency for parties without a naturalist to note mainly the larger mammals and lack of comments about birds does not necessarily signify their scarcity, e.g., "... failure to mention grouse may have been due to their abundance rather than scarceness" (Rogers 1968, p. 11).[1]

6.2.1 The eighteenth century

First published records: Spanish missionaries killed grouse (Bolton 1950; Evans 1997) in southwestern Colorado in 1776, probably blue grouse according to Rogers (1968). Other grouse, however, were found there, and based on characteristics reported, the identification cannot be considered positive. The first virtually certain written record of blue grouse we have found was by Archibald Menzies, surgeon–botanist on Captain George Vancouver's voyage to the northwest coast. Menzies noted, "We here killed some large Grouse which on starting perchd [sic] in the Pine Trees, & we saw some Deer but did not get near enough to have a shoot at them; ..." (Menzies 1790–1797, p. 321). This was at Squirrel Cove, Cortes Island, BC, in July 1792. There can be little doubt that these were blue grouse, for, with two exceptions (recent records of ruffed grouse by ChW Gronau and A Douglas, pers. comm., of which only one is certain), this is the only native galliform recorded on this Island. The ruffed grouse is the only other tetraonine in this region, and which Menzies, coming from Britain, likely would not have considered large.

6.2.2 The nineteenth century

(a) *Meriwether Lewis and William Clark*. Concurrent with early explorations of the west coast by sea were a rapid westward expansion of the fur trade and the beginning of overland expeditions. The next important records of blue grouse occurred during the Lewis and Clark expedition, the first complete crossing of the continental United States. On 21 July 1805, near present Helena, MT, Lewis reported their first sighting:

> "I also saw two fesants [sic] today of a dark brown colour much larger than the phesant [sic] of the U' States" (Moulton 1987, p. 412) [dark brown pheasant was often used in later clear references to blue grouse, "phesant of the U'States" is the ruffed grouse].

and on 1 August 1805, in the general vicinity of Three Forks, MT, he wrote:

> "as I passed these mountains I saw a flock of black or dark brown phesants [sic]; the young phesant is almost grown we killed one of them. This bird is fully a third larger than the common phesant [ruffed grouse] of the Atlantic states" (Moulton 1988*a*, p. 26).

Lewis later described these birds, and although one cannot be sure whether he was describing males or females, they were most certainly blue grouse [black pheasants may have been males, dark brown pheasants, females]. Lewis's nomenclature for blue grouse included black pheasant, large black pheasant, and dark brown pheasant (Coues 1895*a*). As well, he described a large black and white pheasant which Coues concluded was the Franklin's [spruce] grouse (*Falcipennis canadensis franklinii*), but that was clearly the blue grouse.[2]

Lewis provided another description of this grouse, a specimen from the Cascade Mountains. He wrote, on 16 April 1806, near the mouth of the Deschutes River, OR:

> "Joseph Feilds brought me a black pheasant which he had killed; this I found on examination to be the large black or dark brown pheasant I had met with on the upper part of the Missouri. it is as large as a well grown fowl ... the tail is composed of 18 black feathers tiped [sic] with bluish white, ... over the eye there is a stripe of a 1/4 of an inch in width, uncovered with feathers of a fine orrange [sic] yellow. the wide spaces void of feathers on the side of the neck are also of the same colour" (Moulton 1991, p. 126).

This bird was clearly a "coastal" male (based on location, it was *D.o. sierrae*). Lewis also provided a longer and more detailed description of blue grouse while in winter quarters at Fort Clatsop, OR.

Swainson and Richardson (1831) suggested that the descriptions of Lewis and Clark were too vague for scientific purposes. However, although Lewis and his colleagues provided no scientific nomenclature with grouse they described, and caused some confusion because of names used, Coues (1895*a*) and Skaar (1969) argued that they provided the first descriptions of blue grouse, and we agree.

(b) *Zebulon Montgomery Pike*. At the same time Lewis and Clark were pushing westward in the north, Pike was leading an expedition into more southern portions of the Rocky Mountains. On 26 November 1806, he entered the following note in his journal, "On the side of the mountain, we found only yellow [*Pinus ponderosa*] and pitch [*Pinus* sp.] pine. Some distance up we found buffalo [*Bison bison*]; higher still the new species of deer [*Odocoileus hemionus*] and pheasants" (in Jackson 1966, p. 350). Coues (1895*b*) identified the pheasants as dusky grouse and pinpointed the location as Cheyenne Mountain near Colorado Springs, CO.

(c) *Thomas Say*. Although Meriwhether Lewis provided the first known descriptions of blue grouse, Thomas Say is sometimes credited with that distinction (e.g., Swainson and Richardson 1831; Audubon 1840–1844; Baird et al. 1874). Say was an ornithologist with the expedition of Major Steven H Long to the southern Rocky Mountains. The exact date is unclear, but some time between 8 and 10 July 1820, in the vicinity of Defile Creek, in the Colorado Springs, CO area, Say reported:

> "Here met a female bird, which closely resembles, both in size and figure, the female of the black game (*tetrao* [sic] *tetrix*); it is, however, of a darker colour, and the plumage is not so much banded, ... It may be distinguished by the name of Dusky Grouse (*Tetrao obscurus*, S.)" [the first scientific name for blue grouse] (in James 1823, p. 14).

Thus, the southern Rocky Mountain race is recognized as the nominate form of this species. Nevertheless, the bird had been known to fur traders for some 30 years (Swainson and Richardson 1831) and had been generally described by Lewis, though not properly named, some 15 years earlier. It had undoubtedly been known and used by native peoples for millennia. Say provided his description from a female and apparently did not see a male.

(d) *David Douglas*. Douglas, a British botanist, was sent to the New World to collect plants for the Royal Horticultural Society. He explored the Pacific Northwest and travelled across the continent from the mouth of the Columbia River to Hudson Bay, mainly with trappers, fur traders, and Indian guides. An enthusiastic naturalist and collector, his appears to be the first detailed description of the male, from birds obtained from the Hudson's Bay Company by Joseph Sabine. These birds were "... probably taken in the mountains near the sources of the river Athabasca" (Douglas 1829, p. 143). Douglas maintained a daily journal and clearly was aware of the earlier description of blue grouse by Say. Nevertheless, he appears to have used at least five different common names for the species (see 4.1.2), seldom clarifying them with the scientific name, and offered little in the way of descriptions. A sampling of entries from his journal (Douglas 1914) reads like this:

> p. 63 — April to June 1826, at Kettle Falls, WA, on the Columbia River, ". . . *Tetrao Richardsonii* and *T. urophasianellus* were so plentiful that they formed a principal part of food."

> p. 170 — 10 May 1826, overland between Kettle Falls and the Spokane River, "In crossing the mountain just mentioned I killed seven black partridges, the same as the one preserved two weeks since [almost certainly a blue grouse] ... found one nest with seven eggs ... Blew one egg as a specimen and cooked the others; ..."

> p. 182 — 9 June 1826, in a letter to Joseph Sabine, and written at Walla Walla, WA, "I have been fortunate enough to procure two pair of a very handsome species of Rock Grouse, found only in mountainous ground. A male of this species I killed last year on the coast, where they are very rare."

> p. 246 — 8–12 April 1827, between the mouth of the Spokane River, which empties into the Columbia River, and Kettle Falls, "The last three days' journey afforded good sport with gun among the small pheasant [likely ruffed or sharp-tailed grouse], curlew [*Numenius* sp.], and black or mountain grouse, basking on the shores of the river."

Other entries clearly referred to blue grouse, and others may, or may not, have been this species. Since Douglas was aware of the earlier description of the dusky grouse, it is unfortunate he did not use Say's vernacular name.

Back in England, on 16 December 1828, Douglas (1829) described his observations of North American grouse and quail (Odontophorine). Comments of interest respecting *T. Richardsonii* (now *D.o. richardsonii*), which he described (p. 142), include:

> "The voice is a continuation of distant hollow sounds, Hoo-hoo-hoo, like the cooing of a dove [likely the first published description of the song of the male] ... They are easily captured by small snares formed of sinews of the deer tribe. . . Very abundant on the sub-alpine regions of the Rocky Mountains in latitude 52° N longitude 115° W [now in western Alberta]. Still more numerous in the mountainous districts of the river Columbia in latitude 48° N longitude 118° W [Kettle Falls, WA, area] . . . Rare on mountains of the northwest coast."

He described (p. 141) the belly as "light bluish-gray . . .", perhaps the first written suggestion of a bluish cast to this bird. Douglas made valuable early contributions to our knowledge of this species.

(e) *John James Audubon*. Audubon is perhaps the most famous of all North American ornithologists. He never saw blue grouse, however, and relied on the reports of others for his *The Birds of America* (Audubon 1840–1844). He quoted (p. 90), from the notes of JK Townsend:

> "Dusky Grouse, *Tetrao obscurus* . . . First found in the Blue Mountains, near Wallah Wallah, in large flocks in September. Keep in the pine woods altogether, never found on the plains; they perch on the trees. Afterwards found on the Columbia River in pairs in May."

And (p. 91), from information he received from Thomas Nuttall:

> "The Dusky Grouse breeds in the shady forests of the Columbia, where we heard and saw them throughout the summer. The male at various times of the day makes a curious uncouth tooting, almost like the sound made by blowing into the bung-hole of a barrel, *boo, wh'h, wh'h, wh'h, wh'h*, the last note descending into a kind of echo ... From the examination of specimens in my possession, I am persuaded that this species, like *Tetrao Cupido*, has the means of inflating the sacs of bare skin on the sides of the neck, by means of which, in the breeding season, are produced the curious sounds above."

Here is perhaps the first suggestion that the specialized lateral cervical apteria of the male, noted earlier by Meriwether Lewis, might be involved with song and (or) display as in prairie grouse. Audubon's (1840–1844, p. 92) description of the bird noted ". . . the greyish black of the breast passes into blackish-grey, and finally into dull bluish-grey." The bluish hue surfaces again.

(f) *JG Cooper and G Suckley*. Beginning in the 1850s, westward expansion increased dramatically. Boundaries between the United States, Canada, and Mexico were more or less stabilized, and the United States began explorations for transcontinental railways. In the northern Pacific Railroad Survey, Drs. JG Cooper and George Suckley served as naturalists. In the final report on the avifauna, Cooper (in Suckley 1860, p. 219–220) reported:

> "The dusky or 'blue grouse', as it is called in the western country, is common in most of the forests of the

> Territory, . . . This bird, called generally in Oregon the blue grouse, also known as pine grouse, dusky grouse, &c., I met, for the first time, when our exploring party reached the main chain of the Rocky Mountains, where we found it exceedingly abundant, but not more so than in the Blue Mountains of Oregon, Cascade Mountains, and in all the timbered country between the last mentioned range and the Pacific coast. In the autumn, about November 15, they generally disappear, . . . Concerning the whereabouts of this bird during winter there are many opinions among the settlers. Some maintain that the species is migratory, and that they retire to the south, while others say that they repair to the tops of the highest evergreen trees, where, in the thickest foliage of the branches, they pass the cold season in a state of semi-torpor, rarely or never descending until warm weather comes on . . . These birds, at Fort Steilacoom, are very abundant throughout the spring and summer."

Here, to the best of our knowledge, is the first documentation of the name blue grouse. Also, a number of suggestions that if they were not abundant, they were at least common. And, the first suggestion they might be migratory, which is now well established for most populations studied. Coues (1874, p. 398) quoted Suckley from a later work, "This fine game bird is common in Oregon and Northern California, extending in the Coast Range nearly to San Francisco Bay, and in the Sierra Nevada to about latitude 38°."

(g) *Robert Ridgway*. In the years 1867–1869, Robert Ridgway maintained ornithological records during a United States Government geological exploration along the fortieth parallel. He reported (Ridgway 1877, p. 598),

> "The 'Mountain Grouse', or 'Blue Grouse', was a more or less common species on all the ranges clothed with a sufficient extent of pine forests,[3] the existence of which seemed to strictly govern its distribution. It was found on the Sierra Nevada, near Carson City, and on several of the higher ranges of the Great Basin; but it did not occur in abundance until we arrived at the Wahsatch [sic] and Uintah [sic] Mountains, where it literally abounded in certain localities, particularly on the latter range. . . . Although seldom seen in the dense pine forests, we always found these Grouse in their vicinity, usually in the open glades with scattered trees or brush, with thicker woods on either side."

These birds were not necessarily found within the forest, a point now well established for some breeding populations.

(h) *Other observers*: Throughout the 1800s, a miscellany of notes by other observers suggested blue grouse were scarce to abundant in various localities. A sampling of quotations follows:

> JK Townsend, along the lower Columbia River, 1834–1836, "Two species of Grous [sic] (*Tetrao*) are also abundant, the Common Partridge of the States (*T. umbellus*), and another, the Dusky Grous of the Rocky Mountains (*T. obscurus*) . . . It inhabits, plentifully, the interior of the country & is also frequently found here" (Townsend, in Jobanek and Marshall 1992, p. 5).
>
> CH Merriam, in the central Rocky Mountains, 1872, "The species was not abundant, being met with chiefly in the Teton Mountains" (Merriam 1873, p. 698).
>
> WE Strong, during 13 days in Yellowstone National Park, late July and early August 1875, "There is but one game bird found in the National Park, and of this we killed some sixty in all. It is known as the *Tetrao Obscurus*, or Dusky Grouse" (Strong 1968, p. 106).
>
> H Mayer, in the Gore Range, Middle Park, CO, 2 August 1878, "Blue grouse and sage hens were plentiful. Got six grouse with my revolver, shooting at their heads, but missed four" (in Rogers 1968, p. 10).
>
> NH Chittenden, north end of Graham Island, Queen Charlotte Islands, BC, August 1884, "Bear tracks and traps were numerous, but no game was started except [blue] grouse, which were very tame and plentiful" (Chittenden 1884, p. 85).
>
> EA Mearns, in Arizona, late 1880s, ". . . found [blue] grouse abundant in the White Mountains" (in LeCount 1970, p. 1).
>
> H Hague, on Cortes Island, BC, late 1890s, "There was no road to my place for about eight years, only Deer trails. Deer and Blue grouse were everywhere" (Hague 1931, p. 5).
>
> WW Cooke, in Colorado, "Resident, common in the mountains" (Cooke 1897, p. 70).

(i) *Sale in the market*. Blue grouse were sold in the market, for example:

> George Suckley reported, in the late 1850s: "They are brought to market in winter from the mountains near Napa [California], . . ." (in Coues 1874, p. 398).
>
> "The market price for game at Leadville and Aspen (both in Colorado) in the late 1800s either showed this preference or difficulty of harvest, since grouse [presumably blue grouse] brought 50 cents each while saddles of deer [*Odocoileus hemionus*], elk [*Cervus elaphus*], and mountain sheep [*Ovis canadensis*] averaged 7 cents, 9 cents, and 10 cents a pound, respectively (Hoover, unpubl)" (in Rogers 1968, p. 11).
>
> On Vancouver Island, in the Alberni area, in the 1880s, "Salmon [*Onchorynchos* spp.] sold for 3 for $.25, Cod [Gadidae] for $.25, Wild Geese $.25, Mallard Ducks [*Anas platyrynchos*] $.25 a brace, and Blue Grouse $.25 a brace" (Hague 1931, p. 2).
>
> They also reached markets in the east, "For a notice of the occurrence of this species in Ontario, I am indebted to Mr. CJ Bampton, of Sault Ste. Marie, who has fre-

> quently seen it brought into market at that place" (Macoun 1900, p. 199).
>
> And specimen no. 12867 at the Smithsonian Institution has the following note on its tag, "Brought into Montreal in flesh on sled by Canadian from NW—skinned by J Baron." There is no date on the specimen and it likely came to Montreal for sale in the market.

To supply the market, blue grouse must have been a relatively common species, at least locally. Their desirability as an item of food can be attested to by the following:

> Meriwether Lewis, 1805, "the flesh of this bird is white and agreeably flavored." (in Moulton 1988a, p. 27).
>
> David Douglas (1829, p. 142), "Flesh white, excellent."
>
> Thomas Drummond, "Its food consists of various berries and its flesh is very palatable" (in Swainson and Richardson 1831, p. 345).
>
> JK Townsend, "Its flesh is excellent, the color dark—but richer and more juicy than that of the Partridge . . ." (Townsend 1836, in Jobanek and Marshall 1992, p. 9).[4]
>
> George Suckley, "This grouse is a very fine table bird" (Cooper and Suckley 1860, p. 220).
>
> Dr JS Newberry, ". . . the flesh is white, and equal to that of the Ruffed Grouse or American Partridge" (in Coues 1874, p. 398).
>
> Baird et al. (1874, p. 423), ". . . the flesh is said to be very palatable."

One must use care in evaluating such reports, but there can be little doubt that blue grouse were at least locally common and a sought after and desirable source of food over much of their range in the nineteenth century.

6.2.3 The twentieth century

Until 1900, much of the literature concerning blue grouse was of a taxonomic nature, often with a few natural history notes, as mentioned in our preface. Many were speculative or anecdotal. Perhaps the first author to examine in some depth a particular phase in the life cycle of the species was Anthony (1903). He described their peculiar downward migration in spring and upward migration in late summer and autumn (see 17.1.2 for more detail). He noted (p. 26) that the majority of birds in the Lookout and Powder River Mountains, OR, moved out of the forest onto the "bare sagebrush plains" for nesting.

With the major period of exploration over, some expeditions were mounted with the express purpose of investigating natural history. Little was known about some of the more northern areas, and attempts were made to remedy this situation. AE Preble, with M Cary, collected in the Northwest Territories and Preble (1908, p. 337), wrote,

> "The Indian guide reported the species common on the foothills west of Fort Simpson and on all the mountains along the Liard River . . . The next important note on the species that I can find is also by Richardson, who refers to the bird under the name of '*Tetrao Sayi*,' stating that it has not been killed farther north than the Nohhane Bute [sic]."

Another note from the Nahanni River area is of interest:

> "Christmas (1928) was a roaring success . . . After a blue grouse apiece, with cranberry sauce, we moved on to the big thing of the evening—hot cakes richly fried in bear's lard, . . ." (Patterson 1954, p. 191).

Farther west, Swarth (1926, p. 83) collected birds and mammals in the Atlin region of northern British Columbia:

> "It looks as though the subspecies *Dendragapus fuliginosus fuliginosus* must occur northward continuously along the mainland coast of British Columbia and southeastern Alaska, leaving *sitkensis* restricted to an island habitat. In the Atlin region the 'blue grouse' is resident and fairly common at high altitudes."

And, in southeast Alaska, Grinnell et al. (1909, p. 203) observed, "the sooty grouse was found common by the expedition in most wooded regions visited." By about 1930, the northern distributional limits were becoming delineated. As well, various naturalists were refining our knowledge of the local distribution of the species through the publication of regional bird lists.

A few other studies documenting particular attributes of this bird appeared by the late 1930s. Those of special note are as follows: Van Rossem (1925), on flight feathers as indicators of age; Brooks (1926) and Green (1928), on the display of males; Simpson (1935), on breeding them in captivity; and Moffitt (1938), on downy young. All currently recognized races except *D.o. oreinus*, and a number of hybrids with other grouse and the Chinese pheasant, were now described, and numerous taxonomic and distributional revisions had been made. But there were still no in-depth studies of the life history or ecology of the species. The first to attempt such studies were Leonard Wing, James Beer, and Wayne Tidyman, beginning in 1940 and working mainly in northcentral Washington. Here we end our historical review, for the work of these authors will follow.

6.3 Synthesis

Published records of blue grouse began in the late 1700s, when those of European descent began moving into western North America. This bird had undoubtedly been known and used by aboriginal peoples long before this, however, as evidenced by bones in middens that date back to the border between Recent and Pleistocene times (Miller 1963). This grouse was clearly "discovered" by aboriginals several millennia before the arrival of Europeans. Grouse contributed to the aboriginal economy as food, and to various cultural activities. Some recent cultural traditions involving this bird almost certainly were begun prior to the arrival of Europeans, having been passed down through oral tradition, art, song, or dance.

Blue grouse were first clearly identified in the literature in the early 1800s, by Meriwether Lewis, and Thomas Say provided the first scientific description in 1823. During the next 100 years numerous reports, many of a taxonomic, distributional, or life history nature were published, but few represented in-depth studies. From these, however, general distributional limits and some life history strategies, e.g., a "reverse" altitudinal migration, were identified. Suggestions of high densities in some areas, principally interior, were noted. These reports provided a general view of the species, but more comprehensive studies post-date 1925, with the first in-depth ecological studies beginning in 1940.

Endnotes [Chapter 6]

1. Early terminology reflects backgrounds of observers, and prior to scientific descriptions has caused problems of identification. Grouse were often referred to as pheasants or partridge, and common names often differed among observers. Age and sex, or stage of moult, also can cause identity problems, and many non-naturalists, especially, did not provide adequate descriptions of birds they saw. Nevertheless, if used with care, these records often provide information about early distribution and abundance, even though impressions of abundance varied among observers. Unless stated otherwise, we cite only records for which we consider the identifications as blue grouse clear.

2. It is difficult to reconcile "large" with a description of the relatively small Franklin's grouse, and Lewis noted bare cervical apteria, a characteristic conspicuous in male blue grouse only. Coues also erred in ascribing 18 rectrices to Franklin's grouse; the normal number is 16. Lewis reported 18 for the large black and white pheasant (in Moulton 1988*b*, p. 374).

3. Many travelers referred to all conifers as "pines".

4. The flesh of blue grouse is darker than the "white" of ruffed grouse but much whiter than in other American grouse. Comparisons to the latter may explain reports of blue grouse flesh as white.

CHAPTER 7

The Physical Environment

> *Environments vary in both time and space, and the effects of these variations on observations and theories of communities have not always been appreciated.*
>
> JA Wiens (1989)

For purposes here, the environment consists of four major components: (1) *climate*, which may affect individuals directly, or indirectly through its influence on vegetation, water, and other organisms; (2) *geomorphology*, which may affect slope, aspect, altitude, soils, and available nutrients, and through these, vegetation and local climate; (3) *vegetation*, which provides food and cover for heterotrophs and which may influence local climate; and (4) *other organisms*, which may compete with, prey on, or cause disease in the species in question. Other organisms can be members of another species, or conspecifics. Each of the major components may be affected by longitude, latitude, altitude, and, in some cases, season and time of day. They are not mutually independent, and many of the relationships among them are poorly understood. We consider the first three here, leaving other organisms—predators, disease, and interactions with conspecifics—to other chapters.

7.1 Geographic range and the environment

Among the 10 North American tetraonines, only the lesser prairie-chicken (*Tympanuchus pallidicinctus*), two species of sage-grouse, and white-tailed ptarmigan have smaller historic ranges than blue grouse (see range maps in Johnsgard (1983) and Potapov (1985)). Longitudinally, blue grouse are more restricted than all other Nearctic tetraonines except the two sage-grouse. This reflects their being confined principally to the two major western cordilleras: the Rocky Mountains and the Sierra Nevada and Cascade–Coast mountains. They have a broad latitudinal range, however, equal to that of sharp-tailed grouse and exceeding those of all other North American tetraonines except ruffed grouse, white-tailed ptarmigan, and rock ptarmigan. Within this range they occupy a wide spectrum of plant communities and climatic regimes in the breeding season. Winter environments are less variable structurally, but owing to the montane habitats occupied, and their wide latitudinal and elevational range, even they differ, especially in terms of plant species composition (Zwickel and Bendell 1986) and climate. We first examine environments of blue grouse at a general level, then more specifically as based on selected studies.

7.2 Physical features of the environment

7.2.1 Geomorphology

Blue grouse are found from ~105°W to ~138°W, and from ~33°N to ~64°N. They are largely confined to the major mountain ranges of the west but occur as disjunct populations in some nearby isolated ranges.[1] Many of these habitat "islands" may have been first occupied when essentially continuous forest connected them to the main cordilleras (see 4.2.3).

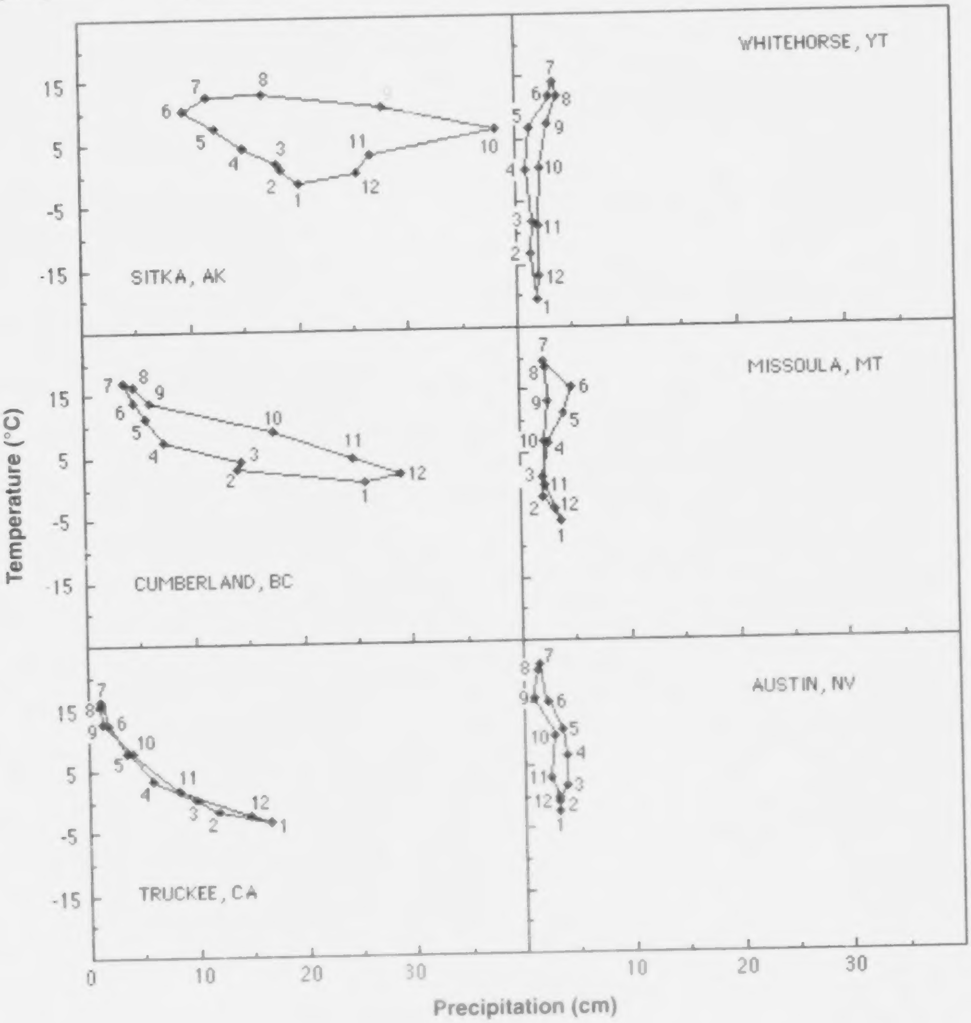
Mountains provide climatic and vegetative heterogeneity, a reflection of broken relief and variations in aspect, slope, altitude, and soils. Montane vegetation also differs with relative proximity to maritime influences. In general, habitats used by this grouse are at lower elevations in coastal than interior mountain ranges, and on western than eastern aspects of the same range. This reflects a shift from maritime to more continental climates and a consequent shift in plant communities as one moves eastward from the Pacific Coast. This gradient is caused mainly by precipitation (Smith 1974).

A latitudinal trend in climate and vegetation, mainly reflecting temperature (Smith 1974), also occurs. In southern areas, e.g., 40°N, occupied plant communities are first found at relatively high elevations, a response to high temperatures and low moisture at lower elevations. In more temperate areas, e.g., 50°N, occupied communities develop at lower elevations. At higher latitudes, e.g., 60°N, alpine tundra replaces montane forest at relatively low elevations, and more or less continuous boreal forest develops below this level. Here, blue grouse are largely confined to the rather narrow ecotone between alpine tundra and montane forest, the subalpine zone (Bendell and Zwickel 1984). They thus occupy progressively higher elevations from west to east and progressively lower elevations from south to north. In montane habitats, grouse can avoid extremes of climatic regimes to some extent by occupying particular aspects, altitudes, and plant communities.

7.2.2 Climate and weather[2]

(a) *Climate.* We used climographs (Landsberg 1958) to examine year-round climatic patterns to which blue grouse are sub-

Fig. 7.1. Annual climographs for selected weather stations over the range of blue grouse, arranged from south (*bottom*) to north. Stations within the range of coastal subspecies are to the left, of interior subspecies, to the right. Numbers represent months. All stations but Austin are based on mean monthly precipitation and temperature records from 1951 to 1980; Austin records, from 1931 to 1950.

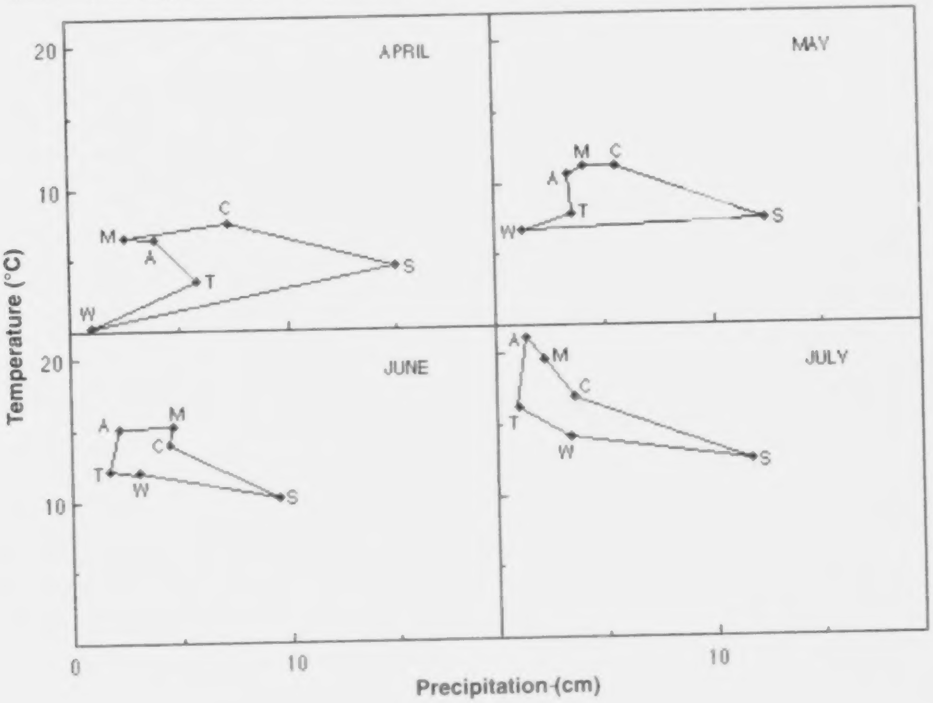


jected in six selected parts of their range (Fig. 7.1).[3] Regimes to which different populations have adapted differ from very warm to very cold and from very dry to some of the wettest on the continent. Annual precipitation is greatest in areas inhabited by coastal subspecies, with interior climates more xeric and, on average, much colder in winter.

Although year-round climatic regimes to which this bird is adapted differ greatly over their range, those in the breeding season do not vary as strongly (Fig. 7.2). In the main breeding period, interior and interior-like climates, e.g., at Truckee, CA, tend to be drier than coastal climates. In north-coastal regions, e.g., at Sitka, AK, precipitation averages approximately two times that, or more, found in other areas in all months. In June and July, mean temperatures at Sitka are also the coldest among stations examined. Even though June, the most usual month of peak hatch, shows the least variation among areas, precipitation at Sitka averages four times, or more, that at Austin, NV, or Truckee. The breeding season climate at Sitka can be described as wet and cool, perhaps wetter than for any other North American grouse. Extensive muskeg within southeast Alaskan forests reflects this cool moist climate. More southern coastal habitats are more temperate.

In contrast, some southern interior birds occupy breeding ranges in some of the hotter and drier montane regions, e.g., near Austin.. They may cohabit shrub-steppe ranges with cacti (*Cactaceae*), rattlesnakes (*Crotalus* spp.), sage-grouse, jackrabbits (*Lepus* spp.), and prong-horned antelope (*Antilocapra americana*). Northern interior breeding ranges, e.g., Whitehorse, YT, are also relatively dry, but cool. In northern regions, blue grouse may cohabit forests and meadows with alpine

Fig. 7.2. Spring–summer climographs for Sitka, AK (S); Whitehorse, YT (W); Cumberland, BC (C); Missoula, MT (M); Truckee, CA (T); Austin, NV (A).



heaths (Ericaceae), gray jays (*Perisoreus canadensis*), willow ptarmigan (*Lagopus lagopus*), spruce grouse, and caribou (*Rangifer tarandus*). At the species level, this bird has adapted to a broad range of climatic conditions in breeding season, perhaps more so than most other species with which they occur.

Winter environments of blue grouse also vary. West-facing slopes of coastal mountains are subjected to high precipitation (Fig. 7.1) that falls mostly as snow above the mean freezing level. In midwinter, at 50°N the freezing level is often at 300–400 m (lower to the north and higher to the south). This results in very heavy snow packs above this elevation, sometimes exceeding 3 m on the ground. Many coastal birds winter in these areas and are confined by snow to a largely arboreal existence. Other coastal birds winter near sea level (Hines 1986*a*; pers. observ.). In some years they may see no snow and be subjected to much rain and mild temperatures. Anecdotal reports and our incidental observations suggest that even these birds are largely arboreal, for they are seldom seen on the ground in winter.

Winter environments in the interior are very dry (Fig. 7.1), with virtually all precipitation falling as snow. Snow packs tend to be much shallower than on the western slopes of the coastal mountains. Temperatures range from moderate, e.g., at Austin, to some of the coldest on the continent, at Whitehorse. At the species level, blue grouse have adapted to a broad range of climatic regimes in all seasons.

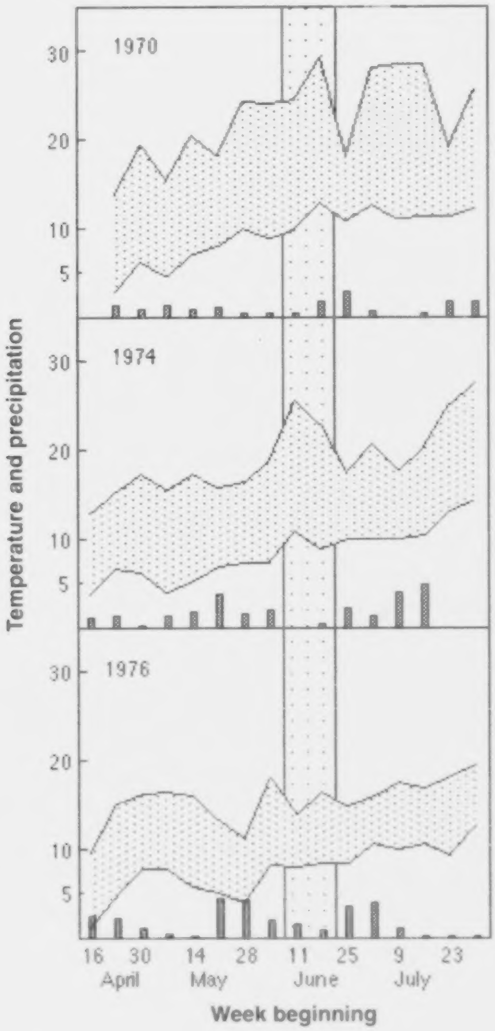
(b) *Weather*. We collected weather data each year at two stations at Comox Burn, 1969–1978. We use records from one station in 1970, the warmest, driest year; 1974, a moderate year; and 1976, the coolest, wettest year, to illustrate variation at this site in the breeding season. This station was located in open, early seral forest that was changing rapidly, and maximum temperatures, especially, may have been partly affected by these changes. In general, mean maximums (usually daytime) showed more variation than mean minimums (usually very early morning), within and among seasons (Fig. 7.3).

With exception of the weeks beginning 25 June and 23 July, 1970 was warm and relatively dry from late April to early August. All weekly mean maximum temperatures but two after the week beginning 21 May exceeded 24°C. Mean maximums reached this level only three times in 1974. At the opposite extreme, no mean maximums exceeded 20°C in 1976. Mean minimums followed the same trends, but with smaller differences. Precipitation fluctuated widely in all years and appears unpredictable in this region.

We operated similar weather stations at Duck Creek (1985), the May Ranch (1985), Skalkaho (1986), and Hudson Bay Mt. (1986).[4] In each case, we have only one year of data so cannot examine within area variation. Nevertheless, differences among areas were so great some conclusions seem warranted.

As at Comox Burn, weekly mean maximum temperatures fluctuated more widely than minimums (Fig. 7.4). Precipitation at all areas was less than, or about equal to, that at Comox Burn in its driest year, 1970. Rainfall fluctuated widely among weeks, ranging from none to over 5 cm. Based on these records, Duck Creek was warmest, and Hudson Bay Mt., a subalpine environment, coolest. Maximum temperatures varied widely among areas, even during peak hatch. Mean maxi-

Fig. 7.3. Mean weekly maximum (upper lines, °C) and minimum temperatures and precipitation (histograms, cm) at Comox Burn$_{cp}$, 1970, 1974, and 1976. Wide vertical bars denote periods of peak hatch.



mums at Hudson Bay Mt. were generally lower than mean minimums at Duck Creek and the May Ranch. Hudson Bay Mt. was cool, perhaps even cold, though relatively dry.

We used peak hatch as a reference point for comparison among areas. Time of hatch is determined much earlier, however. Its antecedent events include ovarian recrudescence (~9 days), copulation (~4 days prior to laying of the first egg), egg-laying (±10 days), and incubation (~26 days). The set point for timing of the breeding season thus occurs ~6 weeks or more before hatch, at a time when temperatures are relatively cool and the ground can be covered by snow.

At both Duck Creek and Skalkaho, spring storms blanketed our study areas with up to 10 cm of snow in the early portions of our field seasons, but new snow at these areas is ephemeral at this season. This was not true at Hudson Bay Mt. On our arrival there, in early May, the entire area was covered with 1–2 m of snow, and only subalpine fir and lodgepole pine were visible as ground cover. Although spring thaw was in progress, occasional storms added up to 15 cm of new snow at a time in early May. On 14 June, we estimated there was still a 50% snow cover in alpine portions of the main study area, and 60%–70% in the forest, with depths up to 1 m in both zones. Leaves of willows (*Salix* spp.) were only beginning to emerge. Heavy snow pack likely contributed to the low temperatures relative to other areas.

In some years, heavy snow packs may occur even at lower elevations in the early part of the breeding season (Fig. 7.5). Even at the local level, blue grouse have adapted to a broad range of temperature, rainfall, and snow conditions in breeding season. This entails, in part, a variation in time of breeding (Zwickel 1977).

7.3 Plant communities occupied

Major plant formations ("biomes") within the geographic range of blue grouse include, from south to north, *low desert*, *shrub-steppe* (high desert), *montane forest*, *taiga* (boreal forest), and *tundra*. Blue grouse may be found at some time of year in all these formations except *low desert*, and perhaps *taiga*. These formations are not homogeneous, however, and each is composed of various plant communities—some are occupied, some are not. We first identify the principal community types that are occupied, then examine how they may be structured, using selected examples for which information is available.

7.3.1 Coastal plant communities

Coastal breeding habitats are those on the Pacific slopes of the Sierra Nevada and Cascade–Coast mountains and those west of these ranges, areas directly affected by maritime influences of the Pacific Ocean. Owing to the restricted longitudinal range of these mountains and the moderating influence of a maritime climate, one might expect birds here to be exposed to less variable climatic regimes and attendant plant communities than interior subspecies. This is only partly true, for *D.o. howardi* and *D.o. sierrae* do not extend to the coast and often occupy xeric interior, or interior-like, environments.

Coastal blue grouse reach their reported southwesternmost extreme in the San Raphael Range—Big Pine Mountain and Reyes Peak (Montagne 1976; Lentz 1993)—near Santa Barbara, CA (Fig. 4.2). At nearby Mt. Pinos, they likely do not occur below about 2400 m in elevation (Pemberton 1928). At this latitude, forests are xeric and interior-like (Fig. 7.6). Little is known of habitat use by *D.o. howardi* except that birds have been reported in association with ponderosa pine, Jeffrey pine, and white fir (J Hamber, pers. comm.; Montagne 1976). These coniferous dominants probably represent the principal breeding habitats from here eastward through the Tehachapi Mountains and other insular populations that may now be extirpated (Bland 2002); also, north and east in the southern Sierra Nevada to ~37°N, where this bird apparently merges with *D.o. sierrae*.

D.o. sierrae occupy forested areas on both sides of the Sierra Nevada. Habitats on the more southern Pacific slopes are xeric and interior-like, those toward the Great Basin, truly interior. In breeding season, this bird may be found in stands

Fig. 7.4. Mean weekly maximum (upper lines, °C) and minimum temperatures and precipitation (histograms, cm) at Duck Creek (1985), the May Ranch (1985), Skalkaho (1986), and Hudson Bay Mt. (1986). Wide vertical bars denote periods of peak hatch.

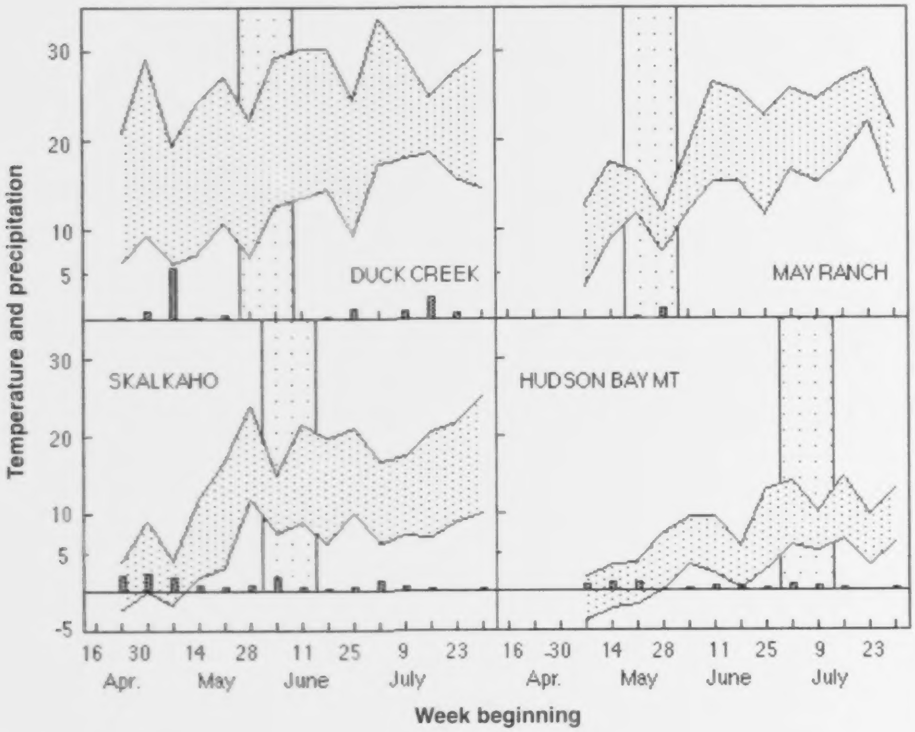


Fig. 7.5. Snow pack at Tsolum Main, 23 April 1971, well into the breeding season. Black spots in snow are tops of stumps, most of which were ≥1 m tall.

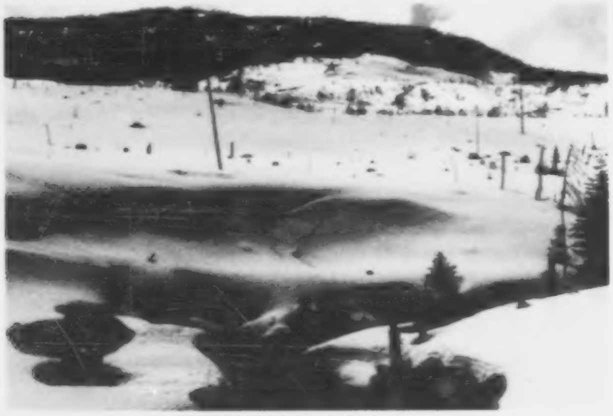
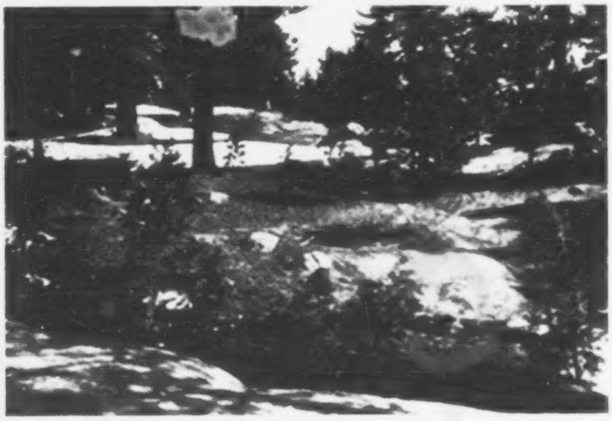


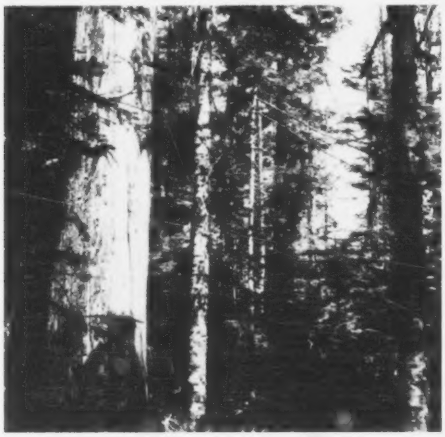
Fig. 7.6. Jeffrey pine forest, Mt. Pinos, CA, 25 May 1978—a xeric and open all-aged forest.



dominated by any of the following species: ponderosa pine, Jeffrey pine, sugar pine (*Pinus lambertiana*), white fir, red fir, Douglas-fir, giant sequoia (*Sequoia gigantea*), and subalpine fir, or various combinations of them. Oaks (*Quercus* spp.) are mid-story associates on some sites. Bland (1997) reported that tree canopies at hooting sites he studied were patchy and dominated by *Abies* and *Pinus*. Stands dominated by ponderosa, or Jeffrey, pine appear to be the lowest elevation conifer communities regularly occupied. Natural meadows are often used as brood range (JD Bland, pers. comm.).

In northcentral California, *D.o. sierrae* merge to the west with *D.o. fuliginosus* and are replaced by them on west-facing slopes of the Coast Range. From about the California–Oregon border north, to their termination near Ellensburg, WA, *D.o. sierrae* are found only east of the crest of the Sierra Nevada–Cascade Mountains, mainly in forests dominated by ponderosa pine and Douglas-fir, but also in suitably open stands of Engelmann spruce (*Picea engelmannii*) and subalpine fir, or various combinations of these species. In contrast to *D.o. obscurus*, *pallidus*, and *oreinus*, *D.o. sierrae* living in

Fig. 7.7. Old-growth western hemlock—Douglas-fir forest, Comox Burn, 23 May 1965—a mesic and dense all-aged forest with many canopy gaps.

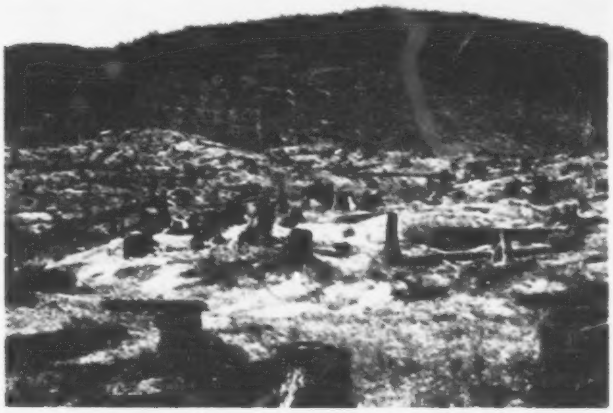


interior and interior-like habitats do not appear to occupy shrub-steppe communities to any degree, but this needs further study.

Northern races of coastal blue grouse, *D.o. fuliginosus* and *D.o. sitkensis*, occupy Pacific slopes of the coastal ranges in northern California, western Oregon, and western Washington, of the Cascade Mountains in Oregon, Washington, and southern British Columbia, and of the Coast Mountains in British Columbia and southeast Alaska. They may breed in virtually all suitably open forest types from sea level to subalpine except, perhaps, parts of the narrow coastal band of redwoods (*Sequois sempervirens*) in northern California and southern Oregon, where anecdotal reports indicate they are rare.

In general, coast forests are much more dense (Fig. 7.7) than those in the interior, and in primeval times blue grouse may have bred there mainly in forest–edge situations, e.g., near natural meadows or rock outcrops, in areas burned by wildfire, or in the subalpine. Nevertheless, they breed in low densities in old-growth forest even now, where they usually are associated with some kind of opening (Niederleitner 1987), e.g., canopy gaps or areas of windthrow. Following clear-cut logging of coast forest in southern British Columbia (Fig. 7.8), they have at times increased spectacularly (Zwickel and Bendell 1985). An increase in breeding density following clear-cut logging appears to be a general phenomenon of coastal birds on some, but not all, areas from western Oregon to southern British Columbia.

Fig. 7.8. Early sere, coast forest clear-cut, Comox Burn$_{cp}$, 10 June 1969.



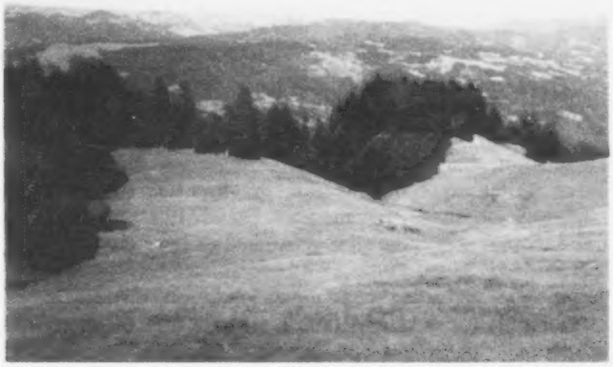
Except for the narrow band of redwoods in California and Oregon, the dominant forest type on the Pacific slope of northwestern California and southwestern Oregon is Douglas-fir (Eyre 1980). Blue grouse likely breed in suitably open forest and forest–edge situations throughout this region, extending into stands of black (*Quercus kelloggii*) and white (*Q. garryana*) oak that may be interspersed with Douglas-fir (Fig. 7.9), and into subalpine forests at higher elevations. Broods often use natural meadows or alpine tundra surrounded by, or at the edge of, forest communities.

Beginning in Oregon, a narrow strip dominated by western hemlock and Sitka spruce is found along the outer coast. This community widens to the north, in western Washington. Douglas-fir dominates most southern Pacific slope forests, however, except at upper elevations, where it is replaced by mountain hemlock, Engelmann spruce, and subalpine fir. Blue grouse here may occupy open forests and forest–edge situations from sea level to the subalpine.

Douglas-fir continues to dominate lowland forest as one moves north into British Columbia, both on the mainland and the southern east-facing slope of Vancouver Island. Here, it is replaced as the major conifer at intermediate elevations by western hemlock, and, at upper elevations, by mountain hemlock and yellow cedar (*Chamaecyparis nootkatensis*). As a lowland dominant, Douglas-fir ends ~175 km north of the Canada–U.S. border and is replaced mainly by western hemlock, mixed with varying amounts of Sitka spruce and western red cedar (*Thuja plicata*). Mountain hemlock and yellow cedar predominate at upper elevations. Breeding birds may be found in varying densities from sea level to upper treeline in any of these forest types.

Various mixtures of western hemlock, Sitka spruce, and western red cedar dominate lowland forests on the west slope

Fig. 7.9. A mosaic breeding habitat consisting of pasture and Douglas-fir forest with an oak border—three distinct plant communities, May Ranch, 1 June 1978. These communities are used differentially by different classes of birds (see Fig. 16.1).



of Vancouver Island. This is the principal lowland forest community from here to the northern extent of the range of blue grouse in southeastern Alaska. Mountain hemlock and yellow cedar predominate at upper elevations. On suitable sites, usually limited, shore pine (*Pinus contorta contorta*) may provide the major forest cover in north coastal British Columbia and southeastern Alaska. Limited study in southeastern Alaska suggests breeding densities are higher in old-growth forest than in clear-cuts (Brown 1966; Doerr et al. 1984; pers. observ.), a relationship opposite to that in some more southern regions (see 16.2.1(a)). Summer range extends from sea level to upper treeline.

7.3.2 Interior plant communities

In southern extremes of the range of interior grouse (i.e., New Mexico and Arizona, Fig. 4.2), conifer forests extend upward only from ~2600 m in elevation. In breeding season, grouse may be associated with a number of forest types dominated by any of the following species: ponderosa pine, white fir, Douglas-fir, Engelmann spruce–subalpine fir, or various combinations of them. Trembling aspen is a common successional pioneer in these communities. Mountain meadows interspersed within the forest and dominated by bunchgrasses and broad-leaved herbs may be used, especially by broods. In general, throughout the range of interior birds, ponderosa pine forest (where present) appears to be the lowest elevation conifer type regularly occupied, although grouse are found occasionally in pinyon–juniper (*Pinus* spp.–*Juniperus* spp.) woodlands (Pekins et al. 1989), just below the ponderosa pine zone.

Further north, in the central Rocky Mountains (Utah, Colorado, and southern Wyoming) pinyon–juniper woodland is replaced by communities dominated by shrubs (especially big sagebrush and bitterbrush), bunchgrasses, and broad-leaved herbs. Interior birds may move well outside the forest into these shrub-steppe areas for breeding, and may reach their greatest interior breeding season abundance in such areas. Subalpine forest is more common than in southern regions, and in addition to conifers further south, bristlecone (*Pinus aristata*), whitebark (*Pinus albicaulis*), limber (*Pinus flexilis*), and lodgepole pine occur at upper elevations. As well as shrub-steppe, blue grouse likely breed in any forest types that are suitably open, principally in those dominated by ponderosa pine and Douglas-fir, but also in successional stands of aspen.

In some areas occupied by disjunct populations, e.g., the Toiyabe Mountains of central Nevada, the only conifer present other than pinyon pine (*Pinus monophylla*) and juniper, neither of which appears to be an important winter food, is limber pine. Limber pine occurs in very sparse, open stands at upper elevations, and the major breeding habitat appears to be shrub-steppe dominated by big sagebrush, savannah-like stands of curlleaf mountain mahogany (*Cercocarpus ledifolius*), and bunchgrasses (Fig. 7.10). Knowledge of these populations is meagre, but an important point is the low diversity and density of conifers available as winter range. Stiver (1994) thinks winter habitat may be limiting to blue grouse in parts of Nevada.

In Idaho, northern Wyoming, and Montana, forests occur at lower elevations, often in the valley floor. Ponderosa pine, Douglas-fir, lodgepole pine, or spruce–fir (Engelmann spruce and subalpine fir), or mixtures of these species, dominate most conifer stands. Principal breeding habitats are in shrub-steppe, ponderosa pine, and Douglas-fir dominated communities, but breeding may extend upward into subalpine–alpine ecotones. This pattern of community structure and occupation persists northward into southwestern Alberta and westward to east-facing slopes of the Cascade and coast mountains in northcentral Washington and southcentral British Columbia.

Fig. 7.10. Sparse limber pine winter range (upper elevations) on a shrub-steppe breeding range, Deep Creek, Toiyabe Mts., NV. Amount of breeding habitat vastly outweighs available winter habitat, opposite to that in most regions occupied by blue grouse.

In the northern Rocky Mountains, first ponderosa pine, then Douglas-fir, drop out (in southern British Columbia and Alberta, and central British Columbia and Alberta, respectively). White (mainly) and black spruce (*Picea mariana*) and lodgepole pine now dominate the forests, including many valley bottoms. Subalpine fir may persist at upper elevations and be mixed with Engelmann or white spruce. Lowland forest canopies are mostly closed and continuous, and in the absence of a low-elevation treeline, grouse are found mainly in the more open subalpine forest–alpine ecotone. White spruce and lodgepole pine are major commercial species and are logged mainly by clear-cutting. In contrast to *D.o. fuliginosus*, birds here apparently do not use these open, early seres to any great degree.

7.4 Breeding habitat

Clearly, blue grouse extract their requirements from a broad spectrum of vegetation types. Since there is spatial and temporal variation within communities, however, a closer examination of habitats occupied is important. Here, we use examples from specific study areas where possible.

7.4.1 Coastal habitats

Most central and north coastal blue grouse breed within single forest communities. These may be more or less homogeneous old-growth stands, or a mosaic of seral stages whose structure and species composition are site or age-specific, but that terminate in the same community. Exceptions are subalpine forests, where alpine meadows occur among open stands of conifers, so-called *parkland* (King 1971), and more northern areas where old-growth forests may border muskeg communities. In contrast, local populations in more southern areas may utilize two or more distinct plant communities (mosaics) in the breeding season.

(a) *Old-growth forest.* Blue grouse breed in lowland old-growth forests (≥250 years since establishment) from northern California to southeastern Alaska, but little work has been done in such areas and our understanding of how these forests are used is limited. In general, coastal old-growth is all-aged and, depending on site, may contain some very large trees. Overhead canopy cover is high but, because of windthrows and standing dead trees, canopy gaps are common. In such gaps there may be a well-developed understory of shrubs and herbaceous plants. Rock outcrops, natural meadows, muskegs, and streams also provide openings within old-growth forest. We think openings are important components that allow blue grouse to occupy these communities.

Niederleitner (1987) studied old-growth forest on Hardwicke Island. The overstory was dominated by large western hemlock mixed with small amounts of western red and yellow cedar, and very small amounts of amabalis fir (*Abies amabilis*), Douglas-fir, and western white pine. The canopy cover by trees was ~75%.[5] The diversity and abundance of shrubs was low (~10% canopy cover), but young trees added another 10% to the shrub stratum.[6] The only true shrub to exceed 5% canopy cover was salal (*Gaultheria shallon*, 7.5%), with red huckleberry (*Vaccinium parvifolium*) next most common. Except for mosses (Bryopsida, 43% canopy cover), the herb stratum was very sparse (canopy cover <1%) on transects sampled. Occasional territorial males and broods were mainly in, or near, openings, and densities were much lower than in nearby post-logging seres (Niederleitner 1987). Niederleitner thought other old-growth stands on Hardwicke had greater canopy patchiness and a better developed herb stratum than areas he sampled (pers. comm., 1990)).

In contrast to Hardwicke Island, Doerr et al. (1984) found territorial males in southeastern Alaska almost solely in old-growth western hemlock–Sitka spruce stands. The tree canopy generally exceeded 65%, with a productive understory of blueberry (*Vaccinium* spp.), dwarf dogwood (*Cornus canadensis*), five-leaf bramble (*Rubus pedatus*), goldthread (*Coptis* spp.), Devil's club (*Oplopanax horridum*), and various ferns (Polypodiaceae).

In the Queen Charlotte Islands, BC, Chittenden (1884, p. 71) reported that blue grouse ". . . were very numerous, and so tame from seldom being hunted, that they would sit upon the branches of the trees almost within reach." This was in lowland old-growth forest prior to significant logging. Clearly, this grouse uses old-growth forest as breeding habitat in some areas and can reach notable densities.

(b) *Post-logging and post-fire seres.* Although blue grouse have adapted to coastal old-growth forest for breeding, they may rapidly colonize very early seral stages following clear-cut logging, and (or) fire (Zwickel and Bendell 1972a; Redfield 1973a). After removal of trees, logging slash may or may not be burned, depending on site, whim of the logging company involved, or government regulations. Productive sites are often converted to conifer plantations, mainly with seedling Douglas-fir in areas south of ~51°N latitude. Most intensive studies of coastal blue grouse have been done in such seral stages that ranged in age from 1 to ~20 years after clear-cut logging or wildfire, mainly on Vancouver Island or nearby smaller islands. Although study areas usually have been within single plant communities, vegetation has varied from even-aged plantations to a mosaic of different aged "natural" seral stages and (or) plantations. We use data from Lower and Middle Quinsam, Comox Burn, and Hardwicke Island to describe young seral habitats used by grouse in this region.

Vegetation on our coastal study areas has varied principally in relation to age of sere after logging or fire. At the time of Fowle's (1960) study at Lower Quinsam, the area had been logged by clear-cutting, beginning as early as 1927 (Bendell 1955*c*). Recall that a 30 000-ha wildfire swept the area in 1938, wiping out all second growth (3.1.1). Fowle measured percent coverage of vegetation on two plots in 1943, 5 years after the fire (Table 7.1). Living vegetation contributed ~55% to the total coverage, the remainder being litter (9%), logs and stumps (13%), or bare ground (23%). Principal herbs were mosses and lichens (Ascomycota), hairy cat's ear (*Hypochaeris radicata*), grasses (Gramineae), vanillaleaf (*Achlys triphylla*), and bracken fern (*Pteridium aquilinum*), in descending order of importance. Principal shrubs (woody species) were trailing blackberry (*Rubus ursinus*), salal, red huckleberry, and thimbleberry (*Rubus parviflorus*), in descending order of importance. Much of the area had recently been planted with seedling Douglas-firs, and they, and seedling western red cedar, the only trees on the sample plots, were minor in terms of cover.

Succession is rapid in lowland coast forest, and by 1950 vegetation at Lower Quinsam had changed markedly (Bendell 1954). From 1950 to 1953, it was characterized by loose to dense associations of willows and red alder (*Alnus rubra*), with ground cover dominated by a mixture of herbs, shrubs, logs, and stumps, interspersed with bare ground. Planted Douglas-firs were ~1 to ~2 m tall in 1950. By 1954 most Douglas-firs, willows, and red alders were more than head-high. The main structural aspect of the vegetation was now tall shrubs and small trees, but with large areas of open space. The canopy cover had strong horizontal and vertical components, and logs and stumps were ubiquitous. The greatest change since Fowle's study was in the advance of woody vegetation. Trailing blackberry, a major berry producer, and hairy cat's ear, a major herbaceous food, were abundant and provided relatively constant coverage. Here, Bendell (1955*c*) reported the highest densities of blue grouse ever recorded.

Bendell and Elliott (1967) described major elements of plant cover at Middle Quinsam in 1962. Recall that they worked there in part because there were two different aged seres (see 3.1.2), one burned in 1952, one in 1938. They classified vegetation into four habitat types, based mainly on height and density of conifers. *Very Open* and *Open* habitats constituted most of the area burned in 1952, *Dense* and *Very Dense* habitats, most of the area burned in 1938. Open and dense types represented areas burned by wildfire 8 and 24 years prior to 1962, respectively (Table 7.1). Trees were a major component of the plant cover, even in open habitats. Herbs were abundant, especially in open habitats. Common species were trailing blackberry, ferns, lichens, hairy cat's ear, pearly everlasting (*Anaphalis margaritacea*), and hawkweed

Table 7.1. Canopy cover (%) of trees, shrubs, herbs, and logs and stumps on study areas on Vancouver and Hardwicke islands in early post-logging seres.

Area, year	Years since logging/fire	Percent canopy cover			
		Trees	Shrubs	Herbs	Logs and stumps
LOWER QUINSAM					
1943	5	<1[a]	12	23	13
MIDDLE QUINSAM					
1962, "open" types	8	30[b]	13	43	13
1962, "dense" types	24	85[c]	27	50	20
COMOX BURN					
1962	1	<1[d]	<1	35	11
1963	2	<1[d]	2	44	11
1964	3	<1[d]	3	42	12
1977	16	34[d]	28	69	6
HARDWICKE ISLAND					
1981	3–13	51[e]	34	39	—

Note: Sources of data: Lower Quinsam (Fowle 1960); Middle Quinsam (Bendell and Elliott 1967); Comox Burn (Zwickel and Bendell 1972*a*) and this study (1977 data); Hardwicke Island (data from JF Niederleitner, analysed by us).

[a] Mainly planted Douglas-fir seedlings, some volunteer western red cedar seedlings.

[b] ~15% conifer, mainly planted Douglas-fir; 15% deciduous, mainly willow, some red alder.

[c] ~60% conifer, mainly planted Douglas-fir and volunteer western hemlock; 25% deciduous, mainly willow, some red alder.

[d] Mainly planted Douglas-fir, small amounts of volunteer western red cedar and western hemlock; most trees were seedling size, 1962–1964.

[e] Mainly planted Douglas-fir or volunteer western hemlock; Douglas-fir dominant on planted sites, hemlock on unplanted sites.

(*Hieracium albiflorum*), in descending order of importance. Salal, bracken fern, and logs and stumps were ubiquitous, but with bracken fern sparse in dense habitats.

We measured vegetation at Comox Burn$_{cp}$ four times between 1962 and 1977 (Table 7.1). In spring 1962, most of the area was barren and dominated by stumps, charred remnants of larger logging debris, bare mineral soil, and ash. The very hot fire of September 1961 had burned most of the humus and smaller logging debris. Some females were, literally, nesting in ashes or on bare soil, with little or no cover other than that provided by logs or stumps (Fig. 7.11). Most of our census plot was replanted with seedling Douglas-firs in 1962 and 1964, but herbs and small shrubs still dominated the landscape in 1965. By 1970, many planted trees were 1 m tall, and other vegetation consisted of a diverse mixture of herbs and shrubs. By 1978, the last year of intensive field work there, many herbs and shrubs were being crowded out by plantation trees, which averaged 3–4 m in height.

We classified vegetation at Comox Burn into several cover types in 1962–1964 (Zwickel and Bendell 1972*a*), based mainly on the most characteristic ("dominant") species in each type. Dominants were all broad-leaved herbs, or herb-like plants (e.g., trailing blackberry). Although herbs were clearly most abundant in all types, the relative importance of different species was changing, e.g., fireweed (*Epilobium angustifolium*), and pearly everlasting cover types increased from 1962 to 1964, the trailing blackberry type decreased, and the thistle (*Cirsium arvense*) type virtually disappeared (Zwickel and Bendell 1972*a*). By 1977, Douglas-fir plantations dominated the landscape. The vegetation was now characterized by clear herb, shrub, and tree strata. Plant composition had changed markedly in terms of both structure and relative abundance of various species of plants. We suspect from general observations that within 5 years of 1977, tree cover would have been 75% or more, the approximate point at which recruitment of blue grouse ends (Zwickel and Bendell 1985). Grouse occupied coast forest of rapidly changing structure (see also Frandsen 1980).

Our study area at Hardwicke Island was composed of a mosaic of different aged seral stages ranging from 3 to 13 years post-logging (Table 7.1). Early seres were similar to those at Lower and Middle Quinsam, Comox Burn, and areas further south, but some plant species had dropped out. Oregon grape (*Berberis* spp.) was rare, and Douglas-fir scarce, except in plantations. This appears to be near the northern limit of these species ranges.

Throughout most of the central coast, common shrubs in early lowland forest seres are salal, willows, Oregon grape, black raspberry (*Rubus leucodermus*), rose (*Rosa* spp.), thimbleberry, salmonberry (*Rubus spectabilis*), and red huckleberry, with ovalleaf (*Vaccinium ovalifolium*) and false (*Menziesia ferruginia*) huckleberry at higher elevations. An attribute of most areas is a high canopy cover of herbaceous plants (Table 7.1). The more ubiquitous herbs in early coast forest seres are mosses, bracken fern, deer fern (*Blechnum spicant*), sword fern (*Polystichum munitum*), wild strawberry (*Fragaria* spp.), fireweed, pearly everlasting, trailing blackberry, hairy cat's ear, hawkweed, and bunchberry. Grasses are ubiquitous, but are generally sparse except in meadow-like situations and are replaced by sedges (*Carex* spp.) on more mesic sites. Although many species are more or less universal in early seral stages, their relative abundance may vary from site to site, with

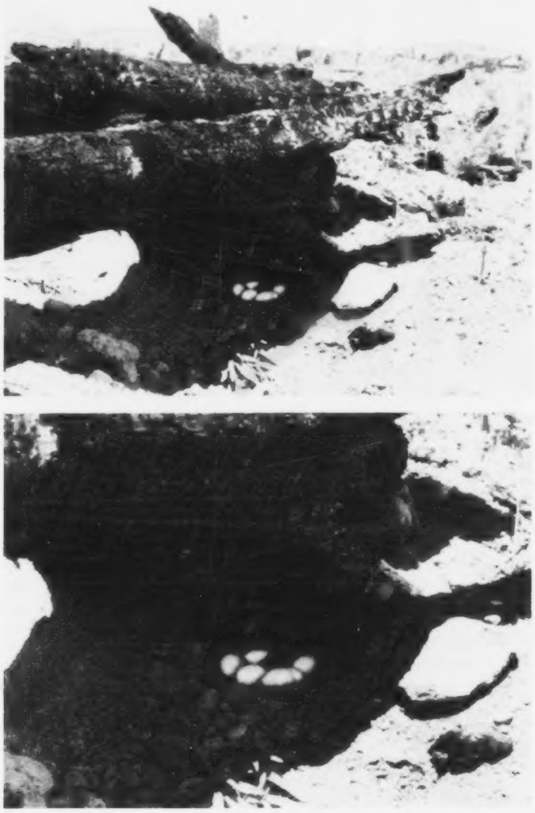


Fig. 7.11. Nest with no lining and only an overhead log for cover, Comox Burn$_{\text{cp}}$, 17 June 1962.

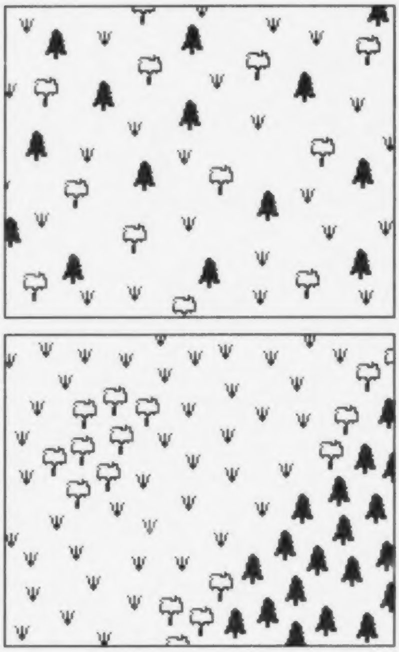


Fig. 7.12. Fine-grained habitat (*top*)—dominant groups of plants are spread more or less evenly over the landscape; and coarse-grained habitat (*bottom*)—dominant groups of plants are clumped as more or less separate communities.

changes in latitude, elevation, aspect, and with the advance of succession. In general, early seres here might be described as "fine-grained"—"everything is everywhere" (Fig. 7.12).

(c) *Coastal community mosaics*. In contrast to north and central coast grouse populations, those in more southern areas may utilize two or more different plant communities in the breeding season. Our study area at the May Ranch (3.1.9) was characterized by four distinct plant communities (Table 7.2). *Pasture*, used mainly for grazing livestock, dominated south-facing slopes. These pastures interface sharply with a Mixed-Evergreen Zone (Franklin and Durness 1973), which was dominated by Douglas-firs and tanoaks (*Lithocarpus densiflorus*) that grew mainly on north-facing slopes and ridge crests at higher elevations. Douglas-firs had been selectively logged at the time of our studies, but many old-growth trees remained. The understory in more dense fir forest was sparse and consisted mainly of sword fern and Oregon grape. More open stands had a mid-story of various mixtures of tanoak, willow, and bigleaf maple (*Acer macrophyllum*). *Oak*, dominated by black and white oak with an understory of grasses, commonly occupied a narrow intermediate zone between the *Pasture* and *Douglas-fir* types. Oak copses occupied some gully bottoms and other mesic sites. On dry rocky areas, a mixture of xeric herbs and shrubs dominated *Scrub* habitats. *Douglas-fir* and *Oak* were heavily treed, with *Scrub* and *Pasture* virtually treeless (Table 7.2). Grouse used all habitat types except *Scrub* at some time in spring and summer and the mosaic pattern of plant associations can be described as "course-grained" (Fig. 7.12).

Little work has been done with *D.o. sierrae* or *howardi*, and we know of only one quantitative analysis of their habitats (Bland 1992; for *sierrae* see 16.2.1(a)). We cannot add more than that and what has been noted above (7.3.1) except to emphasize that these races occupy more open, more xeric, interior or interior-like forests than *D.o. fuliginosus* and *D.o. sitkensis*. At its northern boundary, in central Washington, *D.o. sierrae* occupy essentially the same forest communities as *D.o. pallidus*. Details of habitats of *D.o. sitkensis* are little known beyond those noted above (7.3.1 and 7.4.1(a)).

7.4.2 Interior habitats

(a) *Shrub-steppe*. A major spring and summer habitat of interior blue grouse is composed of virtually conifer-free, shrub-steppe vegetation. The most diagnostic plants on many of these areas are big sagebrush and (or) bitterbrush. Other common shrubs in many areas are black sagebrush, rabbitbrush (*Chrysothamnus* spp.), chokecherry (*Prunus virginiana*), serviceberry (*Amelanchier alnifolia*), Oregon grape, rose, and snowberry (*Symphoricarpus* spp.), and in riparian situations, willow. This is "high desert" and the ground stratum is dominated by various bunchgrasses and xeric herbs, including cacti in some areas. Species composition and relative abundance of

Table 7.2. Canopy cover (%) by trees, shrubs, forbs, or grasses and sedges in main plant communities at the May Ranch, Duck Creek, Skalkaho, and Hudson Bay Mt. study areas.

	Percent canopy cover			
Area, cover type	Trees	Shrubs	Forbs[a]	Grass/sedge
MAY RANCH				
Pasture (47)	<1	<1	3	51
Scrub (10)	4	14	5	31
Oak (9)	68	<1	4	23
Douglas-fir (31)	82	7	15	1
DUCK CREEK				
Big sage (68)	0	34	10	16
Black sage (10)	0	39	6	14
Mountain mahogany (10)	0	60	9	9
Aspen (1)	51	33	14	14
SKALKAHO				
Bunchgrass (23)	0	0	19	18
Ponderosa pine (39)	14	8	12	23
Douglas-fir, thinned (14)	17	10	11	16
Douglas-fir (22)	32	8	12	16
HUDSON BAY MT.				
Apline (41)	0	<1	52	8
Meadow (18)	0	5	62	11
Kruppelholz (14)	3	78	63	<1
Subalpine fir (27)	19	56	58	<1

Note: Percentage of each area in each cover type is in parentheses.

[a] Broad-leaved herbs, including mosses and lichens.

herbs and shrubs often reflect the degree of grazing by domestic livestock. At the more southern latitudes, widely scattered pinyon pines (*Pinus* spp.) and junipers may occur, an exception to the conifer-free generalization.

The principal tree on most shrub-steppe breeding ranges is trembling aspen, usually found in riparian or other mesic situations. Aspen copses often have an understory of shrubs, e.g., snowberry and rose, but which may be excluded by heavy livestock grazing. Aspen can compose a relatively small, but perhaps important, proportion of shrub-steppe breeding habitat of a local population. For example, on the Frazer Creek study area (3.2.3), plant cover types were distributed as follows: shrub-steppe, 87%; oldfield, 11%; aspen, 2%; and pine <1%. There was a tendency here for territorial males to be clustered near aspen copses (Lewis 1985*a*), and hens and chicks used such thickets selectively in late summer (Zwickel 1973).

Our study area at Duck Creek, NV, provides a good example of a shrub-steppe breeding range. Most of the area was dominated by various mixtures of big sagebrush and bitterbrush, with black sagebrush common on crests of major ridges. Widely scattered Utah juniper (*Juniperus osteosperma*) grew at lower elevations. At intermediate elevations, savannah-like stands of curlleaf mountain mahogany graded upward into solid stands of this species. These were replaced at still higher elevations by dense stands of white fir, including some limber pine. Small copses of trembling aspen occupied moist gullies and some creek bottoms. Other riparian vegetation included willow, chokecherry, and flats dominated by giant wild rye (*Elymus gigantus*). We classified the vegetation here into three minor (*White Fir*, *Giant Wild Rye*, and *Riparian*), and four major cover types (Table 7.2). Shrubs were clearly dominant in all major types except *Aspen*, which contributed only 1% to the entire area. Grouse were found in all types except *Giant Wild Rye* and *White Fir* at some time during spring and summer.

(b) *Shrub-steppe–deciduous forest mosaics*. Hoffman's (1981) Eiby Creek, CO, study area (3.2.10) is representative of this habitat. At time of his study, the area was composed of about 55% shrub-steppe and 45% forest. The forest, mainly deciduous, had a tree canopy of about 32%, 91% of which was trembling aspen, 7% thinleaf alder (*Alnus tenuifolia*), and 2% poplar (*Populus angustifolia*) and Rocky Mountain juniper (*Juniperus scopulorum*). Dominant understory shrubs were snowberry, currant (*Ribes* spp.), chokecherry, serviceberry, and rose. Common forbs, broad-leaved herbs, were yarrow (*Achillea lanulosa*), sweet cicely (*Osmorhiza odorata*), meadow rue (*Thalictrum* spp.), dandelion (*Taraxacum officinale*), peavine (*Lathyrus* spp.), northern bedstraw (*Galium boreale*), and chickweed (*Stellaria* spp.). Common grasses were bluegrasses (*Poa* spp.), bromegrasses (*Bromus* spp.), and wheatgrasses (*Agropyron* spp.). Shrubs dominated the rest of the area, principally big sagebrush, serviceberry, and chokecherry, often associated with snowberry, rabbitbrush, and rose. In addition to many of the forbs in forested areas, balsamroot (*Balsamorhiza sagittata*), lupine (*Lupinus* spp.), fleabane (*Erigeron* spp.), larkspur (*Delphinum* spp.), sulfur flower (*Eriogonum umbellatum*), geranium (*Geranium fremontii*), mint

(*Agastache* spp.), violet (*Viola* sp.), and bluebells (*Mertensia* spp.) were common in shrub-steppe habitats. Grasses found in the forested areas, plus Junegrass (*Koeleria cristata*) and sedges, were principal grasses and grasslike plants.

(c) *Shrub-steppe or grass-forb and coniferous forest mosaics.* A third major breeding habitat of interior blue grouse is composed of shrub-steppe or grass-forb associations mixed with ponderosa pine and (or) Douglas-fir forest. These often occur in a mosaic pattern that is dependent on aspect, slope, elevation, and local moisture regime.

Our Skalkaho, MT, study area (3.2.2) was representative of a grass-forb and coniferous forest mosaic breeding habitat. Selective, and a small amount of clear-cut, logging had taken place in parts of the area at the time of our study (1986).

In 1986 we classified vegetation here into one minor (*Riparian shrub*), and four major cover types (Table 7.2). Over 35% of the area, mainly at upper elevations, on north-facing slopes, or in mesic gullies, was dominated by interior Douglas-fir, part of which was seral and had been artifically thinned. Interior Douglas-fir forest is more open than coastal Douglas-fir forest and has a greater abundance of grasses and forbs. Savannah-like stands of ponderosa pine dominated many south-facing slopes at low and mid-elevations. Open stands of pine had an understory of grasses and xeric forbs typical of bunchgrass communities. In stands with more closed canopies, pinegrass (*Calamgrostis rubescens*), elk sedge (*Carex geyeri*), and other herbs dominated the understory. Thickets of Douglas-fir sometimes occupied more mesic sites within pine forest. The most xeric sites, especially south-facing slopes at low and mid-elevations, were dominated by bunchgrasses and forbs. Bluebunch wheatgrass (*Agropyron spicatum*) and Idaho fescue (*Festuca idahoensis*) were the most characteristic grasses, and balsamroot, lupine, fringed sage (*Artemisia frigida*), and yarrow, the most common forbs. Virtually no trees and few shrubs occurred in this community. Vegetation at Skalkaho was mainly a mosaic of two open forest types (~75% of the total area) and a grass-forb community. Grouse used all community types at some time in spring and summer. Martinka (1972) considered seral Douglas-fir thickets to be an important component of the habitat of territorial males. Green Mountain, CO (3.2.10), was typical of a shrub-steppe–conifer forest breeding range.

(d) *Upper elevation montane forest.* Blue grouse may be widely scattered through montane forest types above, or north of, the Douglas-fir Zone, e.g., in mountain hemlock–yellow cedar or spruce–subalpine fir, but little work has been done in such areas. Densities appear low, and birds seem to be associated with openings or edge situations. There is little information about habitats of northern interior birds except incidental observations and anecdotal reports that most birds are found in subalpine–alpine ecotones.

(e) *Subalpine–alpine mosaics.* The upper edge of subalpine forests, the subalpine–alpine ecotone, is more open and parklike than most upper elevation montane forests and is more predictable as breeding range. At northern latitudes, subalpine parklands may serve as the principal breeding habitat of interior blue grouse, but this is poorly documented. This habitat appears to be occupied by breeders throughout the range of the species, although limited evidence suggests grouse densities are low.

We use our Hudson Bay Mt. study area (3.2.14) to represent subalpine breeding habitat. The forest–alpine ecotone there is characterized by alternating upward stringers of alpine fir (mostly as kruppelholz[7]) and downward extensions of alpine meadow or artificially created meadows (ski runs). Alpine meadows and the lower ends of clear-cut ski runs began at ~1550 m and were composed of various mixtures of grasses, sedges, forbs, and occasional patches of low willow. Conspicuous herbaceous plants were Merten's heather (*Cassiope mertensiana*), red mountain heather (*Phyllodoce empetriformis*), pale gentian (*Gentiana glauca*), Arctic lupine (*Lupinus latifolius arcticus*), and Arctic sage (*Artemisia norvegica*). Clear-cut portions of ski runs and small natural meadows within the forest had many of the same species, but more diversity and a greater abundance of shrubs, especially blue and dwarf (*Vaccinium caespitosum*) huckleberry. Arrow-leaved groundsel (*Senecio triangularis*), Arctic sage, mountain arnica (*Arnica montana*), false hellabore (*Veratrum viride*), fireweed, Arctic lupine, sweet coltsfoot (*Petasites frigidus palmata*), and Merten's and red mountain heather were common.

Subalpine fir clothed most of this area below alpine meadows and, including stringers of kruppelholz, extended upward to ~1675 m. This community was composed almost solely of subalpine fir but was mixed with occasional lodgepole pine and spruce at lower elevations. It was mature and relatively open, with an understory of forbs and grasses and a moderate to dense understory of shrubs, mainly blue and dwarf huckleberry. Common ground-level plants were Merten's and red mountain heather, strawberry bramble, Arctic lupine, and colt's foot. Common ground-level plants in the kruppelholz community were colt's foot, strawberry bramble, and Merten's and red mountain heather.

We classified vegetation here into four cover types (Table 7.2). *Alpine* was treeless and almost shrubless, and *Meadow* was treeless, with a low canopy cover by shrubs. In contrast, *Kruppelholz* had a low canopy cover by trees, and high canopy cover by shrubs, most of which was subalpine fir classified as shrub because of its stunted growth form. *Subalpine Fir* had a relatively low canopy cover by trees, but a high shrub canopy, much of which was young subalpine fir. This was open, all-aged forest. All cover types had a relatively high cover of broad-leaved herbs, with grasses and sedges less abundant. Mosses were the most abundant herbs, which generally decreased from more open to more dense habitat types; i.e., *Alpine > Meadow > Kruppelholz > Subalpine Fir*. This area was composed of a mixture of structurally contrasting plant communities, about 40% forested, the remainder non-forested. Although all communities were used by grouse in breeding season, sightings in *Alpine* were few, and most such birds were not far from conifer forest. Among 28 sightings in the alpine, 50% were <10 m, 71% <50 m, 79% <100 m, and 96% <130 m from conifers, principally kruppelholz. One sighting only, at 315 m into the alpine, was >130 m from forest. Skiers report flushing blue grouse here in winter, so this area serves as both breeding and winter range.

In comparison to most coastal populations, interior blue grouse occupy a more diverse array of plant communities in breeding season, often patterned as community mosaics. The most common mix is of more or less treeless shrub-steppe or alpine meadow with deciduous or conifer forest. A common attribute of most interior breeding areas is a high canopy cover

Fig. 7.13. Part of the Frazer Creek study area (in the foreground to top of the ridge beyond the aspen-filled draw), 28 July 1957. By mid to late summer on such xeric breeding areas, herbaceous vegetation is often desiccated, and many grouse begin moving toward forested areas at higher elevations.

of herbaceous plants, but with fewer broad-leaved herbs and more grasses (Table 7.2) than in young coast forest seres. Except in mesic situations and at upper elevations, most herbaceous species are severely desiccated by mid to late summer (Fig. 7.13). Canopy cover by shrubs may be high on shrub-steppe areas but is usually dominated by one or two species. Forest communities range from open savannah-like stands of ponderosa pine to those dominated by more or less closed canopy northern spruces or subalpine fir. In the latter cases, blue grouse seem limited to forest edges, mainly at the forest–alpine ecotone.

7.5 Winter habitats

We have not conducted studies on winter range other than general surveys (Bendell and Zwickel 1984) and examine winter habitats principally on the basis of data provided by others. Most early information is qualitative and anecdotal.

Movement of blue grouse into conifer forest in winter has long been recognized (Anthony 1903; Wing 1947; and see 16.2.2). Most, if not all, birds spend the non-breeding season in such areas (Bent 1932; Beer 1943; Marshall 1946; Caswell 1954*b*; Cade 1985, among others—but see Rogers 1968[8]). This is normal winter habitat for this species.

Some workers have indicated most blue grouse move to high, openly forested ridges to winter (Wing et al. 1940; Marshall 1946; Stauffer and Peterson 1986). On Vancouver Island, King (1971) found virtually all males in upper elevation forest (Fig. 7.14) in winter, but was unable to find hens and chicks. He indicated from this that males and females may be segregated in winter. Others have noted that some grouse winter at lower elevations (Wing 1947; Zwickel et al. 1968), perhaps outside forested areas,[8] but the latter is not well documented.

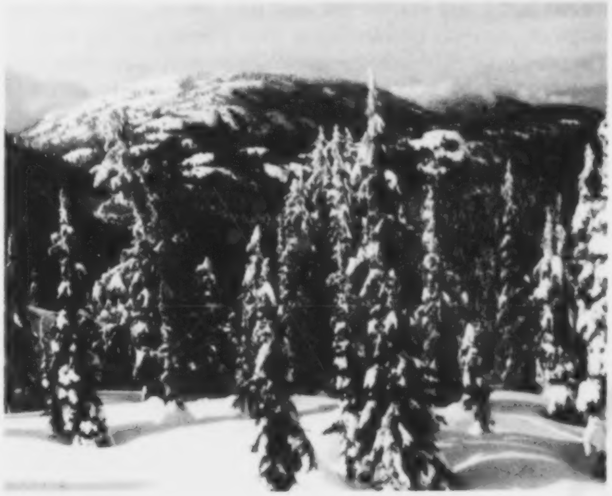
This grouse winters in conifers of a number of different species and at various elevations (Zwickel 1992), some near sea level, even in young second growth (Hines 1987; Cade and Hoffman 1990). Stands may be dominated by any of the following species, alone, or in combination: white fir (Hoffmann 1956), Engelmann spruce–subalpine fir (Cade and Hoffman 1990), Douglas-fir (Beer 1943; Marshall 1946), lodgepole pine (Boag 1958; Cade and Hoffman 1990), limber pine (Zwickel and Bendell 1986), western hemlock (Hines 1987), mountain hemlock (King 1971), and perhaps pinyon pine (Pekins et al. 1989). Other species that may be mixed with these locally are red fir, white spruce, Engelmann spruce, Sitka spruce, yellow and western red cedar, and whitebark, bristlecone, Jeffrey, western white, and ponderosa pine.

We casually noted that as one moved up slope through the Ponderosa Pine Zone and into the Douglas-fir Zone (Daubenmire 1946) in winter in the Methow Valley, that blue grouse were first encountered when the mix of ponderosa pine and Douglas-fir was about 50:50. Here, birds were flushed from thickets of Douglas-fir, whereas below this level, Douglas-fir occurred mainly as single trees. We suspect winter sites are most directly related to the composition and structure of the vegetation rather than to physical characteristics such as elevation, slope, and aspect. The principal feature of forests that might cause variations among stands important to blue grouse in winter is species composition—with attendant variations in height, growth form, density, spacing, canopy cover, and nutritional quality of the trees. These characteristics, alone or in combination, may be relevant to the provision of both food or cover.

Three recent studies provide some detail about winter habitats. Conclusions of special interest were as follows:

Bear River Range. Among 57 winter observations of grouse, 96% were >2285 m in elevation (Stauffer and Peterson 1985). Birds selected open conifer stands with about ". . . a 50:50 conifer cover to open ratio" (Stauffer and Peterson 1986, p. 120). This generally agrees with reports in the literature about winter range being in open forest at high elevation.

Fig. 7.14. Winter range on Vancouver Island. Many grouse winter near upper treeline, far above lower breeding areas. They use isolated trees in the subalpine as well as more dense forest at lower elevations.



Middle Park. Cade and Hoffman (1990), using radio-telemetry, found grouse wintering in a broad range of forest structure, from dense young second growth to open old-growth. Most birds were in Douglas-fir, more females than males. Among 21 birds that left the study areas, 9/9 males and 7/12 females moved into spruce–fir or lodgepole pine stands at higher elevations.

Hardwicke Island. Hines (1987) also used radio-telemetry to study winter habitat use. Young and older grouse used early seres (≤20 years of age) following clear-cut logging, older second growth, and mature forest, a broad range of structural habitats. Evidence of segregation of sexes by elevation (males higher), and perhaps by successional stage, was reported.

The study of Stauffer and Peterson (1985, 1986) tended to support earlier reports about winter habitat, but those of Cade and Hoffman (1990) and Hines (1987) indicated that this grouse uses a wider range of winter habitats than once believed. The latter studies also indicated that males and females may use different habitats, as suggested by King (1971). It is now apparent that many blue grouse do not move to uppermost forested areas. Perhaps earlier suggestions were biased toward particular areas searched, as ridge crests are more easily traversed than slopes in winter. Also, birds may be located and flushed more easily from trees in subalpine parkland than in the less open and generally taller trees at lower elevations.

7.6 Habitat sympatry with other tetraonines

Although geographically limited, blue grouse have adapted to a broad range of plant communities and climatic conditions at the species level, and among and within subspecies. Habitat variations are likely as great, or greater, than for any other North American grouse. We know of areas where they occupy breeding habitat with every other American grouse except the two prairie-chickens, and no other Nearctic grouse has an equivalent degree of breeding season sympatry with other tetraonines (Fig. 7.15). The only clear common denominators that identify all, or virtually all, breeding areas used by this bird are that they have a ground cover with some broad-leaved herbs and shrubs and that they are in, or within the range of, montane conifer forest, their primary winter habitat. The proximity of breeding areas to winter habitat are very likely important in influencing their distribution (Bendell and Zwickel 1984). A rather narrow longitudinal range may reflect their close association with the major cordilleras of western North America.

7.7 Synthesis

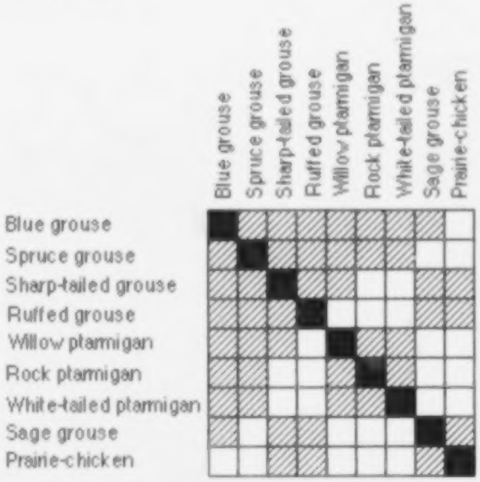
North-coast subspecies of blue grouse inhabit mesic forest of several different plant associations and various aged seres in breeding season, from sea level to subalpine. South-coast subspecies, although clearly related to the northern birds, occupy more xeric interior, or interior-like, forest communities from lower treeline upward into the subalpine.

Breeding habitats of interior birds range from some of the warmest montane plant communities on the continent, including shrub-steppe and various forest communities, to relatively cool subalpine–alpine ecotones. In contrast to more or less temperate coastal habitats, interior temperatures range from hot in the south to cool in the north, with relatively low precipitation, much of it as snow. Many populations inhabit a mosaic of structurally different communities, a mix of shrub-steppe with conifer and deciduous (mainly aspen) forest. This grouse uses a broad range of plant communities for breeding, in terms of both species composition and structure.

Plant communities used in winter are less variable structurally and virtually all populations winter in conifer forest, albeit in a number of different types. This is one of four species of grouse that feeds almost solely on conifer needles and buds in winter, which likely explains their close association with conifers in this season.

Our understanding of winter habitats used by blue grouse is still limited, and for many areas confined to anecdotal reports. We do know, however, that winter habitat varies from relatively mild lowland coast forest with little or no snow, high rainfall, and moderate temperatures to montane coast forest with very heavy snowfall and severe temperatures, to interior montane forest with relatively light snowfall and extreme cold. Although primary winter range has been reported as mature subalpine forest at upper elevations, this grouse winters in forests dominated by a number of different species and at various elevations, some near sea level, even in young second growth.

Fig. 7.15. Sympatry among North American grouse in the breeding season. Cross-hatched squares denote known sympatry between respective species.



	Blue grouse	Spruce grouse	Sharp-tailed grouse	Ruffed grouse	Willow ptarmigan	Rock ptarmigan	White-tailed ptarmigan	Sage grouse	Prairie-chicken
Blue grouse	■	▨	▨	▨	▨	▨	▨	▨	
Spruce grouse	▨	■	▨	▨	▨	▨	▨		
Sharp-tailed grouse	▨	▨	■	▨	▨			▨	▨
Ruffed grouse	▨	▨	▨	■				▨	▨
Willow ptarmigan	▨	▨	▨		■	▨	▨		
Rock ptarmigan	▨	▨			▨	■	▨		
White-tailed ptarmigan	▨	▨			▨	▨	■		
Sage grouse	▨		▨	▨				■	▨
Prairie-chicken			▨	▨				▨	■

Endnotes [Chapter 7]

1. A possible exception to the contention that blue grouse are confined to montane habitats is that they occupy, at least in breeding season, some coastal islands with little relief. Little is known of these populations, however, and these birds may leave the islands in winter.

2. *Climate* refers to generally prevailing weather, averaged over years; *weather*, to the prevailing state of the atmosphere at a particular time and place (Guralnik 1978).

3. We used "normals" from Canadian and U.S. weather stations located in or near occupied range. Records from some stations may not be representative of specific habitats occupied by grouse in the area, but do represent broad climatic patterns for the regions.

4. Stations were located as follows: Duck Creek, ~15 m inside the largest aspen grove on the study area; May Ranch, ~50 m inside old-growth Douglas-fir forest; Skalkaho, in savannah-like ponderosa pine forest; and Hudson Bay Mt, ~20 m inside subalpine fir forest. That at Skalkaho had the most sparse overhead canopy, and that at the May Ranch, the most closed.

5. Quantitative data were supplied by JF Niederleitner but were not presented in this detail in his 1987 paper.

6. Trees <2 m tall were considered as in the shrub stratum.

7. Stunted and twisted trees at upper treeline are most often referred to as krummholz. Gadd (1999) contends this is a misnomer and that kruppelholz is the proper term.

8. Rogers (1968) reported that some blue grouse in Colorado live year round on "brush range", up to 16 km from conifers (no data are presented). M Wickersham (pers. comm.) has heard anecdotal reports of grouse wintering in stands of mountain mahogany in Nevada.

Part 3
Form and Function

CHAPTER 8

Integument

The birds are pre-eminent among vertebrates by virtue of their highly differentiated vestiture with its astonishing variety of structure and colour.

AA Voitkevich (1966)

Most of the integument of birds is feathered, the plumage. Feathers grow in tracts, the pterylae, and help give birds their distinctiveness. In blue grouse they are usually replaced once each year. Bare areas of the integument, such as the apteria, feet, and beak, are much restricted in amount of body covered.

The integument contributes to various physiological functions, to protection of body parts, and especially in birds, to locomotion. It also contributes to inter- and intra-specific recognition and interactions with conspecifics and other organisms, thus having important behavioural implications.

8.1 Plumage

The plumage of yearling and adult blue grouse is strongly sexually dimorphic, with subtle differences between age classes. It varies geographically and serves as a major basis for describing subspecies. Clark (1899) is the only person to have studied positioning of the pterylae of blue grouse in any detail, and judging from his Figs. 1 and 2, they are much as described for ruffed grouse (Bump et al. 1947). He noted (p. 642) that generic differences in pterylae within the galliforms are ". . . as a rule, of slight importance".

Plumages of blue grouse are described in many works (Swainson and Richardson 1831; Coues 1887; Hoffmann 1927; Pearson 1942; Peterson 1961; and Johnsgard 1983, among others). Most authors emphasize the male, describing the female only cursorily. Ridgway and Friedmann (1946), however, provide detailed descriptions of both sexes, as based on *D.o. sitkensis*, and give briefer comparisons of other subspecies to that race. We present general descriptions of natal, juvenal, postjuvenal (First Basic, or yearling), and adult (Definitive Basic) plumages and refer the reader to Ridgway and Friedmann for detail.

8.1.1 Natal and juvenal plumages

In their first summer, chicks acquire three overlapping plumages: natal, juvenal, and postjuvenal (Figs. 8.1, 8.2). By mid autumn they are completely clothed in postjuvenal plumage. See 11.3.1 for transitions from natal to juvenal and postjuvenal plumages.

(a) *Natal plumage.* Chicks are covered with natal down (neosoptile feathers) at hatch. Ridgway and Friedmann (1946, p. 75) described the natal plumage of *D.o. fuliginosus*:

> "Forehead, cheeks, chin, throat, and the underpart of body vary from ivory yellow to straw yellow, the crown mottled with fuscous-black and strongly washed with pale ochracheous-tawny; auriculars sparsely blotched with fuscous-black; the back is pale ochraceous-tawny mottled with fuscous and ochraceous-buff; . . ." [colours are those of Ridgway (1912)].

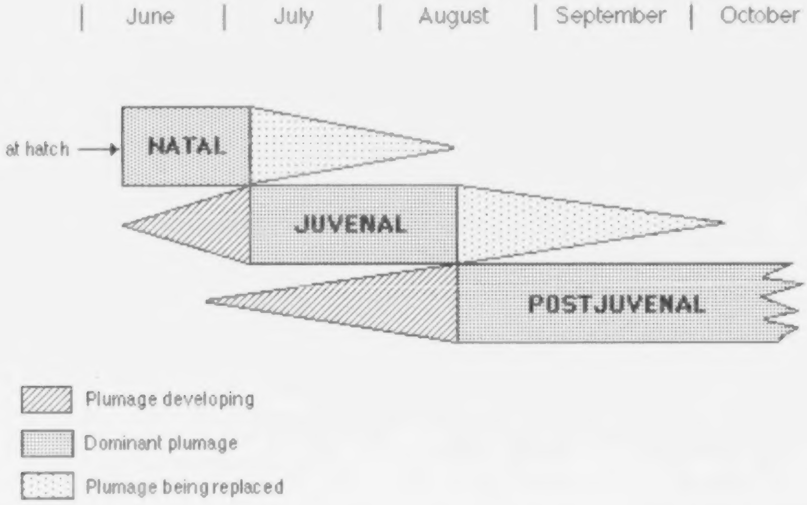
In general, newly hatched chicks of coastal subspecies tend to be brownish yellow ventrally and on the head and neck, but with top and sides of the head mottled with dark browns or blacks. The background colour varies between about Straw Yellow (colour 56 of Smithe 1975[1]) and Tawny Olive (223d). The back is mottled with various shades of reddish (approaching Robin Rufous (340)) and darker browns.

Moffitt (1938) and Ridgway and Friedmann (1946) provide comparisons of natal plumages of various races, but we think there is sufficient individual variation that subspecific identifications would be difficult. Nevertheless, downy young of interior races are ". . . essentially grayish birds ventrally, a consistent difference from the yellowish chicks of the *fuliginosus* group" (Moffitt, p. 594–595). The ventral surface of interior downys we have examined varied between Light Neutral Gray (85) and Pale Neutral Gray (86). Moffitt suggests (p. 595) for coastal and interior forms, ". . . browns and reds predominate in specimens from humid or heavily forested regions as compared with those from more arid localities, which are paler in general coloration . . ." Overall, the hue of interior chicks is grayish, of coastal chicks, yellowish (Fig. 8.3).

We have detected no differences in natal plumages between the sexes, and chicks of all races lack the distinct crown patch characteristic of many downy tetraonines. Mottled patterns on the head and back show much individual variation and are most like those of young sage-grouse and capercaillie. They may serve as cues to individual recognition.

(b) *Juvenal plumage.* This plumage has been described only cursorily. The most comprehensive description is perhaps that of Ridgway and Friedmann (1946, p. 74–75) for *D.o. fuliginosus*:

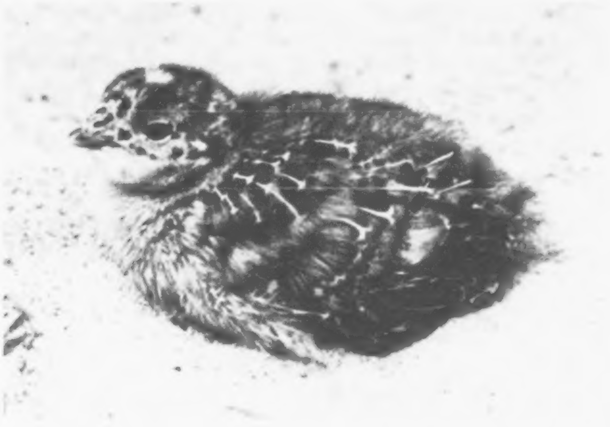
Fig. 8.1. Approximate timing and overlap of juvenal and postjuvenal plumages in a chick's first summer and autumn, Comox Burn.



> "... similar to the adult female of the present subspecies but with the feathers of the interscapulars, scapulars, upper back, lower throat, breast, upper abdomen, and sides with white shaft streaks; chin and upper throat more whitish, less heavily marked with brown and the brown feather tips paler; breast and abdomen paler—buffy whitish to pale tawny white, the breast, sides of abdomen, and flanks spotted with dusky and pale buff; rectrices narrower and more pointed, mottled like the feathers of the back and with no gray terminal band; remiges barred, mottled, or flecked with pale grayish buff on the outer webs" [especially primaries P6–P8].

We have seen differences from this description for some birds from Vancouver Island. Breasts of some juveniles may be quite dark with more blackish than brownish mottling. Chin feathers may be an off-white with no other marking. Two characteristic features are white shaft streaks on distal halves of the rectrices and gray rather than white underwing coverts as in yearlings and adults. Reddish brown feathers (close to Chestnut (32)) extend from the upper beak well onto the crown of juveniles, extent varying among individuals. These are the last contour feathers to moult as this plumage is replaced. Ridgway and Friedmann note some subtle differences among subspecies but indicate they are minor, or non-existent. Juvenal plumages likely are not sufficiently distinct to identify individuals to subspecies, but this needs study.

Fig. 8.2. Chick of ~10–12 days of age in mostly natal down, but with juvenal feathers on shoulders and wings, a mix of two plumages.



Neither Ridgway and Friedmann (1946) nor McFetridge (1972) found differences between juvenal plumages of males and females. The earliest criterion for separating sex by plumage of which we are aware appears in the postjuvenal plumage (see 11.3.4).

8.1.2 Postjuvenal (First Basic) and adult (Definitive Basic) plumages

(a) *Males.* Postjuvenal and adult plumages of males are generally similar and Medium Plumbeous (87) to Blackish Neutral Gray (82). The overall hue is bluish to blackish gray (Fig. 8.4), depending on subspecies. Interior races are more bluish (paler) than coastal birds, and within each group, southern subspecies are paler than northern.

Contour feathers tend to be darkest on the head, back, and upper breast, the background shade and degree of darkness varying among subspecies. Most feathers of the head and neck are solid coloured, and those of the chin and throat are darkish gray, flecked with white. Feathers of the middle and lower back, upper tail coverts, and upper wing surface have light gray vermiculations, often blended with soft shades of brown, extent varying among individuals and subspecies. Darkish gray upper breast feathers lack vermiculations and blend into slightly lighter gray or bluish gray in the mid-breast region. They are generally unmarked and continue unchanged along the ventral surface to the area of the vent, where they may be

Fig. 8.3. Interior downy chick, *D.o. obscurus*, Centennial Ridge, WY (*top*), and coastal downy chick, *D.o. fuliginosus*, Comox Burn (*bottom*). Chicks ~3–4 days of age.

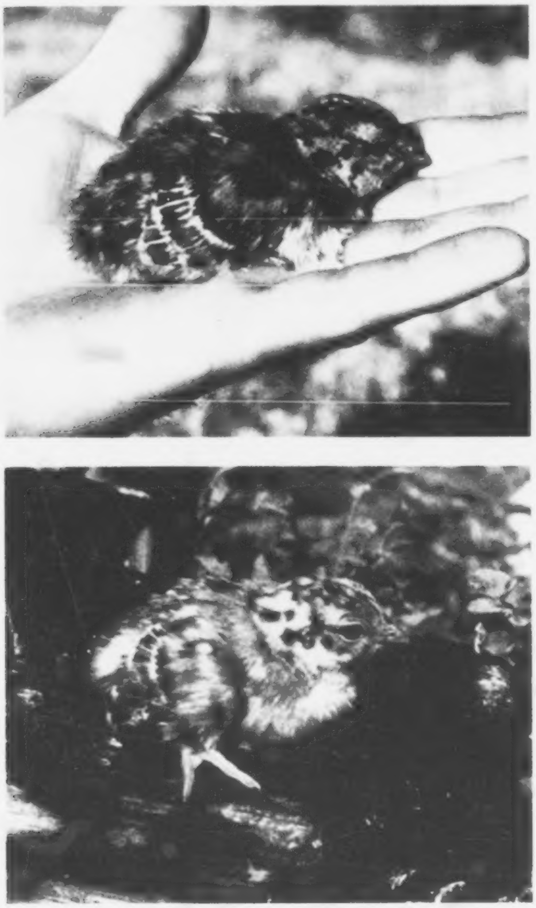
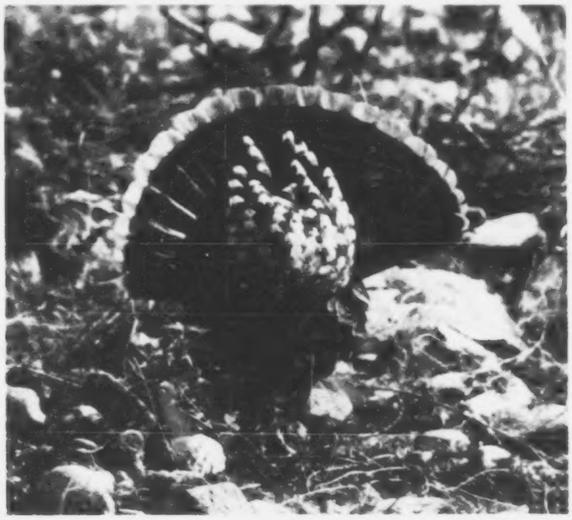


Fig. 8.5. Crissum of an adult male, *D.o. fuliginosus*, in full display, Comox Burn.



narrowly tipped with whitish gray. Those of the flanks are gray of the abdomen and may be narrowly striped with white along and on each side of the rachis, some with white tips. The gray ventral surface (occasionally with some white mottling) contrasts weakly with the soft brownish cast of the gray or blackish gray back and wings. Gray of the abdomen colours feathers of the upper leg and dorsal and lateral surfaces of the tarsometatarsi, but the latter have a slight brownish cast in some individuals. Very short tarsometatarsus-coloured feathers occur on small webs at apices between the toes. Under tail coverts, the crissum, are blackish, sometimes mottled with gray, or grayish, sometimes mottled with black, and broadly tipped with white (Fig. 8.5). The extent of black, gray, and white varies among individuals and subspecies. Colours of the crissum may be important in courtship display.

Fig. 8.4. Interior and coastal adult males in partial display: *D.o richardsonii*, southwestern Alberta (*left*, photo by Wayne Lynch) and *D.o. fuliginosus*, Comox Burn (*right*). Note differences in tail bands and colours of the cervical apteria. Combs are the same colour in both groups.

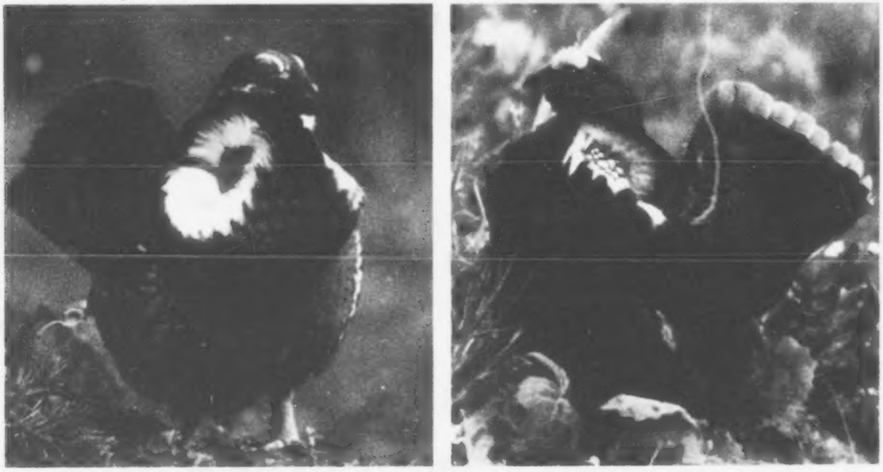


Fig. 8.6. Exposed cervical apteria of a male *D.o. fuliginosus* in feather spread display, Comox Burn. Note strongly tuberculate nature of the apteria.

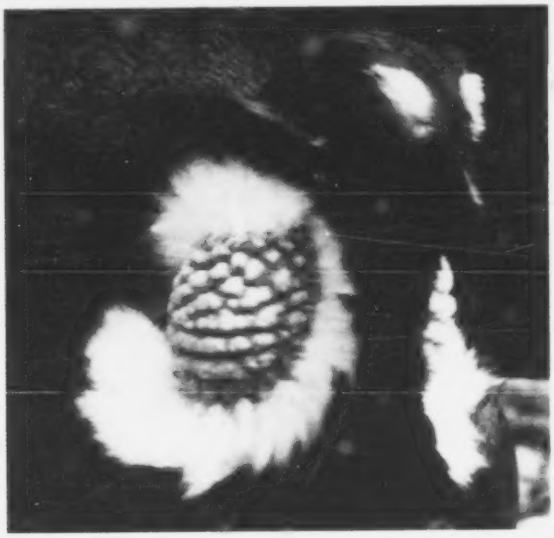
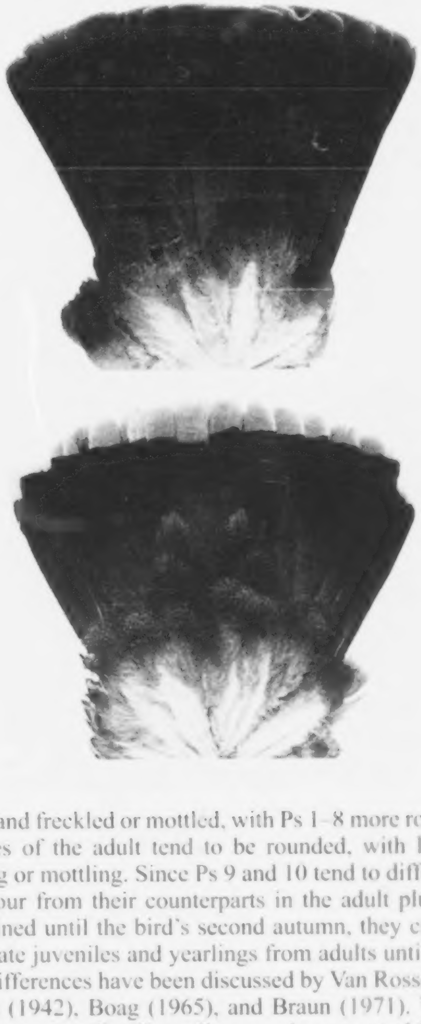


Fig. 8.7. Tail of an interior adult male, *D.o. pallidus* (*top*), Methow Valley, WA, and of a coastal adult male, *D.o. fuliginosus* (*bottom*), Vancouver Island. Note the truncated rectrices and less distinct tail band of the interior bird as compared to the more rounded rectrices and very distinct tail band of the coastal bird.



Lateral cervical apteria[2] of the male, highly specialized for display (Fig. 8.6), are ringed by white feathers (Caswell 1954*a*) tipped with the same gray or blackish gray as the surrounding contour feathers. The white is not visible if the body feathers are sleeked but may show as a fine white line if feathers of the neck are partly raised, a condition often evident during routine singing (Bendell and Elliott 1967; McNicholl 1978).

Flight feathers of the wing, the primaries and secondaries, range from Olive-Brown (28) to Medium Neutral Gray (84) or Dark Neutral Gray (83). Under wing coverts are mostly white, but gray toward the leading edges. Lumsden (1970) noted that all tetraonines have white lesser wing coverts on the underside of the proximal end of the humerus. These are normally out of sight but in interactions with other grouse, or humans, may be exposed as a "white shoulder-spot" (McNicholl 1978; Jamieson 1983*b*; and see 15.2.3(i)).

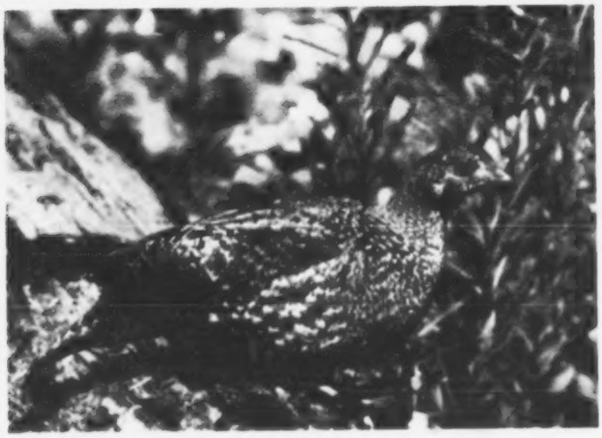
The proximal two-thirds of the rectrices tend toward Blackish Neutral Gray, blending toward Jet Black (89) more distally. All races except *D.o. pallidus* and *D.o. richardsonii* have a distinct terminal tail band that ranges between Light Neutral Gray (85) and Dark Neutral Gray and contrasts sharply with the more proximal blackish background (Fig. 8.7). The tail band may be speckled with black, amount varying among individuals, perhaps among subspecies. It is indistinct or absent in *D.o. pallidus* and *D.o. richardsonii*, and if present, tends toward Blackish Neutral Gray.

The postjuvenal plumage is attained while birds are classified as juveniles. Feathers of the back and wings may have more of a brownish cast than in adults, a result of more brown mottling, but the overall hue is still bluish to blackish gray. Two characteristics will almost always separate yearlings from adults. The bird's first primaries (Ps) 9 and 10 are not shed in the prebasic moult, but juvenal Ps 1–8 are replaced, a characteristic of all native North American galliforms (Dwight 1900; Van Rossem 1925). Primaries 9 and 10 tend to be pointed at the tips and freckled or mottled, with Ps 1–8 more rounded. All primaries of the adult tend to be rounded, with little or no freckling or mottling. Since Ps 9 and 10 tend to differ in shape and colour from their counterparts in the adult plumage and are retained until the bird's second autumn, they can be used to separate juveniles and yearlings from adults until that time. These differences have been discussed by Van Rossem (1925), Petrides (1942), Boag (1965), and Braun (1971). With some experience, virtually all yearlings can be separated from adults on the basis of these differences.

A second character is almost as reliable for separating yearlings from adults and often will confirm age if differences in primaries are not clear. Postjuvenal upper tail coverts of yearlings are marked by more or less random gray or grayish brown flecking, with whitish gray, narrow bars on a blackish background (Nietfeld and Zwickel 1983).[3] Upper tail coverts of adults lack the whitish gray bars, and gray or grayish brown flecking, if present, occurs in a more vermiculated pattern.

Van Rossem (1925) first noted that rectrices of yearling blue grouse are shorter and narrower than in adults, especially in males. Bendell (1955*b*) measured lengths and widths of outer rectrices of yearling and adult male *D.o. fuliginosus* and found no overlap between age classes. Lengths separated age

Fig. 8.8. Female plumage is much more cryptic than that of the male.

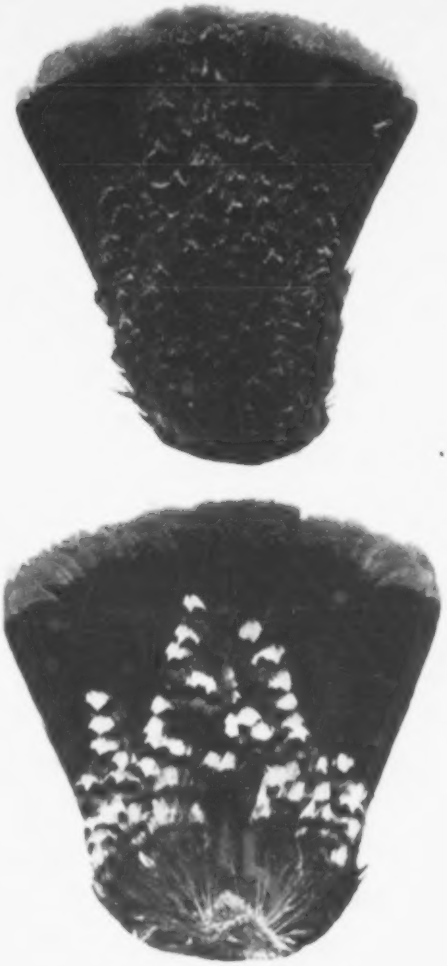


classes better than widths. Boag (1965) found no overlap in lengths or widths of rectrices of yearling and adult *D.o. richardsonii* or *D.o. pallidus*.

(b) *Females*. Postjuvenal and adult plumages of females are much mottled with various shades of gray, brown, and white (Fig. 8.8). The overall hue of coastal females is brown, not blackish or bluish gray as in males. This results from a mixture of colours such as Blackish Neutral Gray or Dusky Brown (19) with lighter browns such as Russet (34) or Army Brown (219b). The hue of interior females is more grayish, a mixture of dark grays such as Blackish Neutral Gray tempered with soft browns such as Drab (27) and (or) light grays similar to Glaucous (79). Interior females are more similar in general colour to interior males than are coastal females to coastal males, but are much mottled as compared to the more or less solid bluish gray of the male.

Contour feathers tend to be darkest on the back, shoulders, and upper surfaces of the wings. They are banded with narrow to moderate transverse stripes of light shades of gray, brown, or grayish brown, depending on race. Feathers of the head, neck, and upper breast are similar to those of the back but generally lighter in hue. Brown bars on the upper breast are broader than on the back. Feathers of the chin and throat are brown or gray, flecked with variable amounts of white, and in some individuals may be buffy white mottled with soft brown. White feathers that surround the lateral cervical apteria of the male are "barred grayish-brown" in the female (Caswell 1954*a*, p. 139). Feathers in the shoulder region may have small triangular whitish tips that extend proximally a short way down the rachises. Brownish breast feathers blend abdominally into more or less solid gray that continues to the area of the vent where they may be narrowly tipped with white. Whitish tips may occur on other ventral feathers, providing a whitish mottling against a gray background, but there is individual variation. Feathers of the flanks are mottled with browns or grays with narrow white stripes along and on each side of the rachises. Some are tipped with white. Solid gray of the abdomen colours feathers of the upper legs. Those of the tarsometatarsi are short and gray or grayish brown. Very short tarsometatarsus-coloured gray or grayish brown feathers are present on small webs at apices between the toes. In general, brown mottling of interior races is paler than in coastal races, but there is variation even within local populations and among subspecies.

Fig. 8.9. Dorsal (*top*) and ventral (*bottom*) views of a coastal female tail, *D.o. fuliginosus*. Note brown barring on the central rectrices and upper tail coverts, distinct tail band, white-tipped under tail coverts (the crissum), and rounded tips of the rectrices, typical of coastal birds.



Primary and secondary remiges of females tend toward Olive-Brown. Under wing coverts are mostly white, mottled with grays and browns toward their leading edges. White lesser wing coverts on the underside of the proximal end of the humerus can be exposed dorsally to produce a white shoulder-spot, as in males.

In contrast to males, the two central rectrices are transversely banded, with alternating black (or dark brown) and light brown bars (Fig. 8.9). Light brown bars may extend onto some of the more lateral rectrices, but these feathers are usually more or less solid blackish, or very dark brown. Females of all races but *D.o. pallidus* and *D.o. richardsonii* have distinct terminal tail bands, Medium Neutral Gray or Dark Neutral Gray, but these bands are often obscured on the two central feathers. When present, the tail band is often flecked with black dots, and its leading edge is less sharp than in males. The tail band is indistinct or absent in *pallidus* and *richardsonii*. Upper tail coverts are banded with alternating black, or very dark brown, and light brown bars, a contrast to the fine vermiculations on the upper tail coverts of adult males. Under tail coverts, the crissum, may be barred with alternating black, brown, and (or) gray, and are broadly tipped with white. Even within local populations, the basic hue of the undertail coverts may be primarily black, brown, or gray, with white tips.

The yearling plumage of females is, in general, indistinguishable from that of adults. Nevertheless, age classes can almost always be separated by differences in the relative shapes and colours of Ps 9 and 10—pointed in yearlings, rounded in adults (as in males). Yearling upper tail coverts of females differ from those of males (Nietfeld and Zwickel 1983), but there appears to be no age class difference within females.

In contrast to male *D.o. fuliginosus*, lengths of outer rectrices of yearling and adult females overlap (Bendell 1955*b*). Boag (1965) too found lengths of outer rectrices of yearling and adult females (*D.o. richardsonii* and *D.o. pallidus*) to overlap. Length of rectrices is not, therefore, a valid criterion for assigning age to females.

All colours of both sexes vary with time since replacement, for they change with both fading and wear.

8.1.3 Geographic variation in rectrices

Distal ends of the rectrices of coastal blue grouse tend to be rounded and those of interior subspecies more square, or truncated (Fig. 8.7), giving the partly folded tail a roundish appearance in coastal birds and a more squarish appearance in interior birds (Baird et al. 1874; Van Rossem 1925; Swarth 1926; Bent 1932; Ridgway and Friedmann 1946). These are fair generalizations but are subjective, difficult to quantify, and may not have been examined adequately for all races (Swarth suggests they may vary with age). Some geographic differences do not conform to the coastal–interior classifications, e.g., distinctness of the tail band, width of the tail band (if present), and numbers of rectrices.

(a) *Tail bands.* Blue grouse can be separated into two groups on the basis of presence of a distinct tail band, or presence of an indistinct, or absence of, a tail band. Baird et al. (1874, p. 421–422) described this character for coastal and southern Rocky Mountain birds as "... with a distinct terminal band of clear plumbeous", and for northern Rocky Mountain birds as "... without any terminal lighter band, or else having it badly defined" (Fig. 8.7). Subspecies included in the first group are *D.o. obscurus*, *D.o. oreinus*, *D.o. howardi*, *D.o. sierrae*, *D.o. fuliginosus*, and *D.o. sitkensis*, and in the second group, *D.o. pallidus*, and *D.o. richardsonii*. This character is widely recognized as a distinction between these groups (Bent 1932; Ridgway and Friedmann 1946; Johnsgard 1983). To test this generalization, we classified museum specimens as to presence or distinctness of tail bands (Table 8.1).[4] Those of all *D.o. obscurus*, *D.o. oreinus*, *D.o. howardi*, *D.o. sierrae*, *D.o. fuliginosus*, and *D.o. sitkensis* were distinct. Those of *D.o. pallidus* and *D.o. richardsonii* were not significantly different from each other [1], and >99% (410/413) were absent or indistinct.[5]

Table 8.1. Yearlings and adults with distinct, indistinct, or no tail bands among subspecies (by %).

Subspecies	Distinct band	Indistinct band	No band
Northern interior[a]	<1 (3)	77 (320)	22 (90)
Southern interior[b]	100 (85)	0	0
All coastal[c]	100 (251)	0	0

Note: Data are from 749 museum specimens; includes both sexes. Sample sizes are in parentheses.
[a] *D.o. pallidus* (*n* = 262) and *D.o. richardsonii* (*n* = 151).
[b] *D.o. obscurus* (*n* = 81) and *D.o. oreinus* (*n* = 4).
[c] *D.o. howardi* (*n* = 39), *D.o. sierrae* (*n* = 71), *D.o. fuliginosus* (*n* = 87), and *D.o. sitkensis* (*n* = 54).

Width of tail band varies among subspecies, tending to decrease from south to north (Swarth 1926; Ridgway and Friedmann 1946). We measured widths of bands of yearlings and adults from museum specimens to examine the relationships between sexes, age classes, interior and coastal subspecies, and among subspecies (Table 8.2). In all groups tested, tail bands were significantly wider in males than females [2, 3]. Within males, bands of adult *D.o. pallidus* were wider than in yearlings [4] (larger samples of yearlings from other subspecies are necessary to test this relationship more rigorously). Among females, in four subspecific comparisons, there were no differences between adults and yearlings [5]. Widths clearly differ among subspecies [6a–d, 7a, b, 8a–f]. Where differences do not occur, they involve subspecies with contiguous latitudinal ranges, in some cases, those that might be considered as "supersubspecies" (see 4.1.2(c)). In all cases involving differences, tail bands of more southern groups were wider than those of contiguous groups to the north, confirming that they tend to decrease in width from south to north.

Tail bands also tend to be wider in interior than coastal subspecies at equivalent latitudes [9a, b, 10]. In adult males, however, that of *D.o. howardi*, the southernmost coastal race, was wider than in combined *D.o. pallidus* and *D.o. richardsonii*, the two northernmost interior subspecies [11a]. That of adult female *D.o. howardi* did not differ from adult female *D.o. pallidus* [11b] or *D.o. richardsonii* [11c]. Thus, although tail bands of interior birds tend to be wider than in coastal birds at equivalent latitudes, there is overlap between northern interior males and *howardi*, the most southern coastal birds.

In summary, tail bands are (1) wider in males than in females, (2) likely wider in adult than yearling males but with no difference between adult and yearling females, (3) wider in interior than coastal subspecies at the same latitude, but with an overlap between northern interior and southern coastal races, and (4) they show a strong tendency to be wider in southern than northern birds.

(b) *Numbers of rectrices.* Some early literature reported that blue grouse have 20 rectrices (Swainson and Richardson 1831; Coues 1887; Ridgway and Friedmann 1946). However, Clark (1899) and Short (1967) provided evidence for variation in the numbers of rectrices among subspecies. According to Short, *D. o. pallidus*, *D.o. richardsonii*, and *D.o. oreinus* tend to have

Table 8.2. Widths of tail bands (mm, means ± SE, and ranges) among subspecies.

Subspecies	Yearling male	Adult male	Yearling female	Adult female
D.o. obscurus	27±1.6 (7)	31±0.4 (37)	22±1.3 (8)	24±0.8 (19)
Range	20–32	25–37	18–30	16–30
D.o. oreinus		27 (1)		24±1.9 (3)
Range				20–26
D.o. pallidus	18±0.5 (21)	19±0.4 (64)	16±0.5 (39)	17±0.4 (56)
Range	13–23	13–28	9–23	10–23
D.o. richardsonii	17 (1)	20±0.5 (29)	14±0.8 (13)	15±0.5 (36)
Range		13–25	10–20	9–20
D.o. howardi	15±3.8 (3)	21±0.6 (23)	12±2.0 (2)	17±0.9 (10)
Range	8–21	17–29	10–14	13–22
D.o. sierrae	13±0.9 (5)	17±0.8 (21)	12±1.2 (9)	14±0.5 (24)
Range	10–15	11–25	6–17	8–17
D.o. fuliginosus	16±1.3 (6)	16±0.5 (33)	13±0.7 (12)	13±0.4 (28)
Range	13–21	12–23	9–16	10–17
D.o. sitkensis	13±0.6 (5)	15±0.5 (20)	13±0.9 (10)	12±0.6 (17)
Range	11–14	12–20	9–17	9–17

Note: Width of band was measured along the rachis of one central rectrix in males and because the proximal border of the band is often obscure on the central rectrices of females, along the rachis of a rectrix immediately laterad to a central rectrix in females. Birds without bands were not included in computing means or expressing ranges. Data are from 558 museum specimens. Sample sizes are in parentheses.

20 rectrices, *D.o. obscurus*, *D.o. howardi*, *D.o. sierrae*, *D.o. fuliginosus*, and *D.o. sitkensis*, 18. Clark examined only *D.o. obscurus*, *D.o. fuliginosus*, and *D.o. richardsonii* and reported the same tendency for these groups, respectively. Following on Short's study, and combining his work with theirs, Zwickel et al. (1991) reported the modal number of rectrices for all coastal subspecies and *D.o. obscurus* as 18 (80% with 18), and the modal number for *D.o. pallidus* and *D.o. richardsonii* as 20 (70% and 81% with 20, respectively) (Fig. 8.10). A relatively small sample of *D.o. oreinus* ($n = 32$) was equally divided between birds with 18 or 20, making a decision for this race unclear. Caswell (1954*b*) reported a mode of 20 (81% incidence) among 87 *D.o. pallidus* from Idaho. With exception of the unclear picture for *D.o. oreinus*, modal numbers of rectrices among subspecies parallel the pattern shown by distinctness or indistinctness–absence of tail bands, i.e., coastal subspecies and *D.o. obscurus* normally have 18 rectrices and distinct tail bands, *D.o. pallidus* and *D.o. richardsonii* normally have 20 and indistinct, or no, tail bands. These characters appear to be linked. Blue grouse are the only tetraonine with a clear distinction in normal numbers of rectrices among subspecies and have a range in number of 16–22 (Zwickel et al. 1991).

Short (1967, p. 8) suggested that males and females might differ in numbers of rectrices but considered the degree of difference "not marked". Zwickel et al. (1991) found in all cases tested (coastal subspecies combined, and *D.o. fuliginosus*, *D.o. pallidus*, and *D.o. richardsonii* separately) that males and females had the same modal numbers of rectrices. There were no significant differences between the sexes, although most birds with submodal numbers were females, and most with supermodal numbers, males. In one presumed subspecific "hybrid" population, *D.o. fuliginosus* × *D.o. richardsonii*, males and females differed significantly in modal numbers—males 20, females 18. There is, thus, some tendency for females to have fewer rectrices than males.

8.1.4 Plumage anomalies

(a) *Albinism* (leucism). Albinism was first documented in blue grouse by Braun and Blumberg (1973), in an immature male shot near Mesa Seco, CO. They reported (p. 345) this bird was "very pale gray" throughout and considered it an "imperfect albino". In other respects, it appeared normal, with black bill, toenails, and eyes, and "dark horn-colored" feet. External measurements were normal.

Crawford (1987) examined wing and tail collections of 1996 blue grouse shot by hunters in northeastern Oregon and found an adult male and an immature male with some partly white rectrices and upper tail coverts, an incidence of 0.1% albinism. The adult also had a few white feathers on the back and upper rump. Crawford also described a partly albinistic adult male from northeastern Oregon in the collection of the Department of Fisheries and Wildlife at Oregon State University. This bird was mostly white but with bill and feet of normal colour.

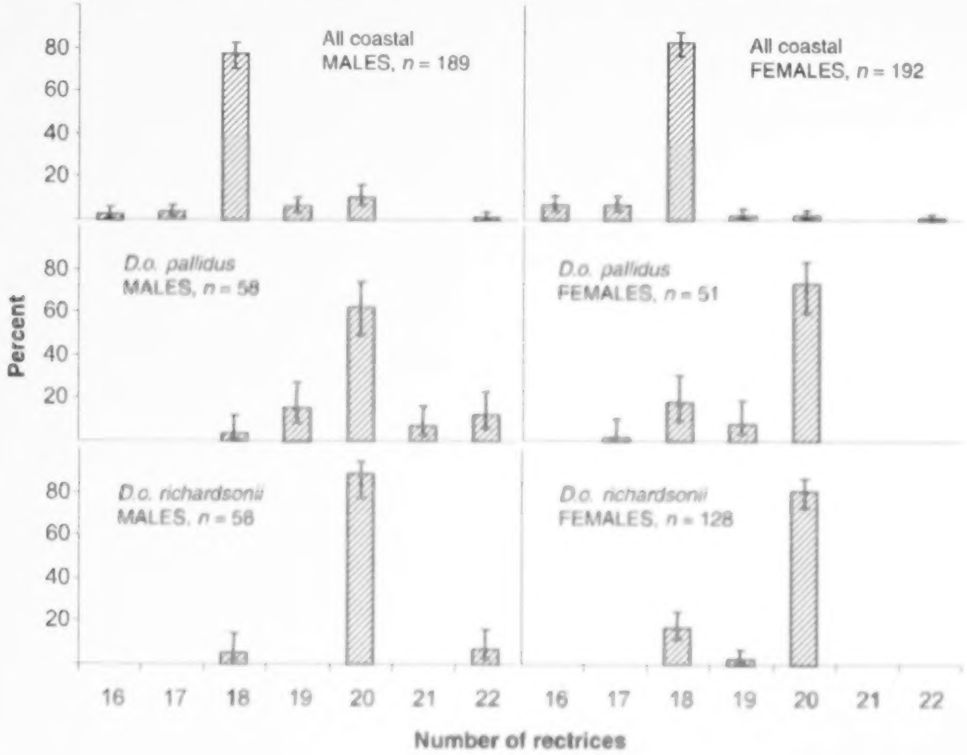
We add the following incidences of albinism, extracted from field notes:

No band, juv, sex?, summer 1952 or 1953—white juvenal primaries, Beavertail Lake, BC.

5376, ad fem, 29 Jul 1971—medial claws on each foot white, outer claws black. Comox Burn.

5402, juv, sex?, 2 Aug 1971—outer vane on juvenal P8, left wing, mostly pure white; outer juvenal bastard quill, left wing, pure white. Comox Burn.

Fig. 8.10. Variation in the numbers of rectrices of coastal and northern interior blue grouse (by %). Adapted from Zwickel et al. (1991, copyright by the Wildlife Society). Includes one bird with 15 rectrices.



5501, ad fem, 6 Aug 1971—white spot on front of neck. Comox Burn.

10331, ylg mal, 28 May 1974—P10, left wing, all white; outermost primary covert, right wing, all white. Comox Burn.

11284, ad fem, 8 Jul 1976—white, 8 mm diameter circle on back of head. Comox Burn.

12072, ylg mal, 5 Jun 1979—P10, right wing, all white. Hardwicke Island.

These birds, all partial albinos (Gross 1965), were identified in a sample of 6629 individuals handled in coastal British Columbia, an incidence of 0.1%, identical to that reported by Crawford (1987). We noted no albinism among 729 other grouse banded or collected in various areas, coastal and interior. Albinism appears rare in blue grouse, as reported for ruffed grouse (Bump et al. 1947).

We also examined 2313 specimens in 34 museums throughout North America and noted colour anomalies when seen. We found two clearly albinistic specimens, those documented by Braun and Blumberg (1973) and Crawford (1987). A third specimen, no. 9109 at the Royal British Columbia Museum, Victoria, BC, borders on albinism. This adult female was collected on Vancouver Island, 16 September 1945. Its basic hue is very light brown or tan, closest to Drab (27), with Olive–Brown (28) rectrices, primaries of Light Drab (119C), some with white tips, and a ventral surface nearest to Glaucous (80). A clear tail band, approximating Pale Neutral Gray (86), is apparent. The beak most closely approaches Fawn (25), and the bird had no dark brown mottling, very unusual for females in this region. Mottling is apparent, but all colours appear diluted, and this may be an imperfect albino.

In addition, specimen no. 393075 in the Smithsonian Institution collection is likely an albino blue grouse. This downy chick, collected in Sequoia National Park, CA, 2 July 1933, is "very white" [our notes], with, because of the strange colour, some question as to species. Judging from the location and the unlikely probability of any other tetraonine in the area, we think it a blue grouse.[6]

(b) *Other plumage anomalies:*

We have seen one melanistic specimen. A juvenile female, no. 15083 in the JR Slater Museum of Natural History at the University of Puget Sound, Tacoma, WA, has no white mottling on the breast or flanks. Areas normally mottled white are sooty gray, although other colours seem unaffected. This may be imperfect or partial melanism.

Standing (1960) collected an adult female in the Methow Valley with white, rather than gray, feathers surrounding her lateral cervical apteria.

Occasionally a bird is seen that has not replaced all its primaries in the previous moult. The usual situation is a bird with nine adult primaries and a heavily worn and faded postjuvenal P10 on each wing; in one instance, on one wing only. We interpret this as retention of postjuvenal P10 during the first postnuptial moult, and classify these birds as adult. The incidence is perhaps one or two cases among several hundred birds processed each year.

We have found four birds with odd numbers of primaries: a juvenile male, an adult male, and an adult female, each with 9, and an adult female with 11. Those with nine had no empty feather follicles.

About 8% of all blue grouse have an uneven number of rectrices (Zwickel et al. 1991), an anomaly first noted by Short (1967). Most birds with an uneven number have 19, intermediate between subspecies with 18 or 20. Significantly more birds from a presumed subspecific hybrid population, *D.o. fuliginosus* × *D.o. richardsonii*, had an uneven number (mostly 19) than non-hybrid populations. Uneven numbers may result mainly from a mixing of this character between races normally having 18 or 20.

"Fault bars", transverse weak spots across the vanes and shafts of rectrices, are occasionally seen in birds captured in the wild. In some cases feathers may be broken off at the sites of these bars. They are more common in aviary birds and usually involve all rectrices of an individual. In aviary chicks, we suspect they may have occurred at the time birds were handled for weighing, perhaps a result of the stress of handling.

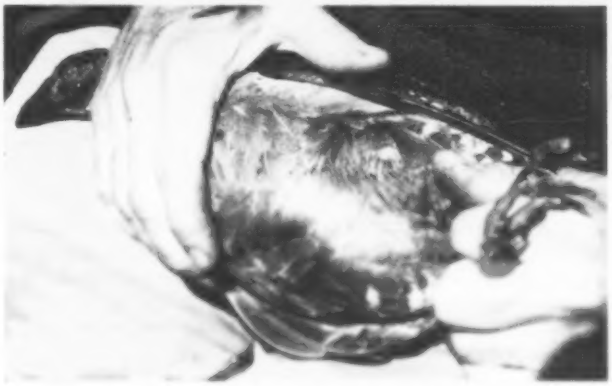
Other anomalies include an adult male collected on 22 May with vanes worn off the proximal half of most rectrices, two yearling females captured on 20 May and 29 July, in which the distal half of all, or most, postjuvenal rectrices had been broken off, and a yearling female with all rectrices except the outer pair barred with alternating dark and light browns—only the two central rectrices are normally so coloured. Lastly, Bendell (1955*b*) marked two males with printers ink in May 1952, and one still had ink on one primary, most secondaries, and some underwing coverts in June 1953, indicating an incomplete postnuptial moult in 1952.

It is not uncommon to find a bird with one or more, rarely all, rectrices, or patches of contour feathers (most often on the rump or back), being replaced outside the normal period of moult. Such replacement is likely a result of accidental or predator-induced loss of feathers. These should not be considered anomalies.

8.1.5 Moult

Moult is defined by Van Tyne and Berger (1966, p. 574) as the "renewal of plumage" and includes the loss (ecdysis) and replacement (endysis) of feathers. That of North American tetraonines was first considered in some detail by Dwight (1900). He noted that in general there is little difference among the genera or species of grouse; a principal exception being the ptarmigan. Following attainment of the postjuvenal plumage, most species, including blue grouse (Lucas and Stettenheim 1972), pass through a complete, or near complete, postnuptial moult that begins in mid to late spring and is completed in autumn. Dwight suggested that there may be a minor prenuptial moult in some species in early spring but did not detect it in blue grouse; nor have we seen such evidence. Once the postjuvenal plumage is attained, there is only one complete, or near complete, plumage change each year, the postnuptial moult.

Fig. 8.11. Fully developed brood patch of an incubating female, Vancouver Island.



No one has described the entire sequence of feather replacement in blue grouse, although some authors have reported on replacement in particular feather tracts, or have provided generalized views of the moult. We use these works and our studies to provide some understanding of this process (see also 11.3.1 for plumage changes in juveniles). We first consider the brood patch, a special case.

(a) *Brood patch.* The brood patch is a seasonal apterium of the lower breast and abdomen of incubating females and those with small chicks (Fig. 8.11).[7] It includes the sternal apterium, and after loss of feathers, skin of the abdominal pterylae. It also likely includes posterior regions of the sternal pterylae, and upper and inner parts of the crural pterylae. It develops as a result of the loss of virtually all feathers in the lower breast and abdominal regions and is accompanied by oedema and increased vascularization of the skin, presumably to facilitate transfer of heat from the hen to eggs and chicks and to control water loss of the eggs during incubation.

Bump et al. (1947) suggested that the brood patch of ruffed grouse develops as a result of feathers being plucked from the sternal and abdominal pterylae. More recent evidence indicates, for birds in general, these feathers are shed under hormonal influences (Payne 1973), although exact mechanisms are poorly understood. We suspect the latter for blue grouse.

Among females examined for gonadal development, we have seen no feather loss in the abdominal pterylae prior to laying of at least two eggs. Hens with 4–7 postovulatory follicles (POFs) had only partial feather loss in the brood patch area (Table 8.3). Among 35 females with an egg in the oviduct at time of collection, 10 had partial brood patches and 25 had none. Two examined at, or about, day 2 of incubation, and 16 examined at ≥3 days of incubation had full brood patches. Clearly, the brood patch develops during laying and is completed by, or shortly after, onset of incubation, as suggested by Bendell (1955*c*). Earliest dates that we have detected brood patches were 3 May at Comox Burn and 30 April at Hardwicke Island. By 4 June at Comox Burn (Fig. 8.12), and 21 May at Hardwicke, most females had detectable brood patches. The pattern at Hardwicke was similar to that at Comox Burn, but ~2 weeks earlier.

From 1972 to 1977, we described post-hatch refeathering of brood patches of 51 females at Comox Burn, summarized as follows:

Table 8.3. Numbers of females moulting brood patch feathers compared to numbers of postovulatory follicles (POFs) in their ovaries. Data from Comox Burn and Hardwicke Island combined.

Number of POFs	Number of birds	Number moulting	Percent moulting[a]
0–3	29[b]	1[c]	3
4	9	4	44
5–7	6	5	83
8	2	2	100

[a] All birds but those with eight POFs had partially defeathered brood patches. Those with eight POFs had fully developed brood patches, and ovaries indicated they were incubating.

[b] 21 had at least one POF, i.e., they were laying.

[c] This bird had two POFs.

(1) No refeathering in 33 hens with chicks between ~1 and 10 days of age.

(2) Pinfeathers only, or vanes were just beginning to emerge on nine hens with chicks between ~8 and 15 days of age.

(3) Vanes on new feathers were ~2 cm long on nine hens with chicks between ~12 and 28 days of age.

(4) Refeathering was ~50% complete on four hens with chicks between ~25 and 40 days of age.

(5) Refeathering was more than two-thirds complete on six hens with chicks between ~40 and 60 days of age.

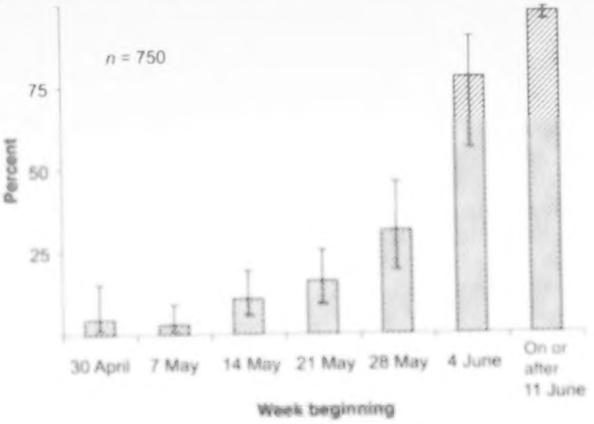
There is some overlap between age categories of chicks because of variation among females and difficulties in describing feather replacement under field conditions. Nevertheless, replacement pinfeathers usually appear in the second week following the end of incubation,[8] and most females ~60 days post-hatch have replaced all feathers of the abdominal pterylae.

Brood patches are clearly detectable on most females on Vancouver and Hardwicke islands until 15 July but after that can often be detected only by careful examination. Including both areas, 10% of 78 brood females and 64% of 28 lone females examined for brood patches in the first 2 weeks of August had completely refeathered abdominal pterylae, and 20% of 41 brood females and 79% of 29 lone females examined in the latter half of August had replaced all feathers of the brood patch. Thus, refeathering is complete, or nearly complete, in most females in this area by mid to late August. New feathers are clearly recognizable by their rich colour and unworn condition as compared to the worn and faded feathers of the previous body moult.

(b) *Postnuptial moult*. The postnuptial moult involves loss and replacement of the postjuvenal (First Basic) and all subsequent plumages. In contrast to loss of feathers of the brood patch, old feathers are displaced by newly growing feathers beneath them (Voitkevich 1966; Payne 1973). Replacement of those of the wing (Dwight 1900) and entire plumage (Johnsgard 1983) approximates the pattern described for the change from juvenal to postjuvenal plumage (11.3.1–11.3.3). Moult normally begins with the loss of P1.

Bendell (1955*b*) provided a general description of the postnuptial moult of *D.o. fuliginosus* at Lower Quinsam. Primaries of yearlings and adults began to moult by the last week of May, beginning at the wrist and proceeding distally. By end of June, moult was underway in the head and neck region and extended over the back, sides, and legs. By end of July, P5 and P6 were being replaced, and by August and early September P7 and P8 were regrowing. Rectrices began to shed in mid to late August, were replaced from the outside mediad, and were fully replaced in most birds by mid September. Bendell suggested a complete annual moult may not always occur.

Fig. 8.12. Females with brood patches (in %), by week (includes yearling and adult females), Comox Burn, 1969–1978. On or after 11 June includes the 5 weeks ending 15 July, with weekly percentages ranging from 91% to 99%.

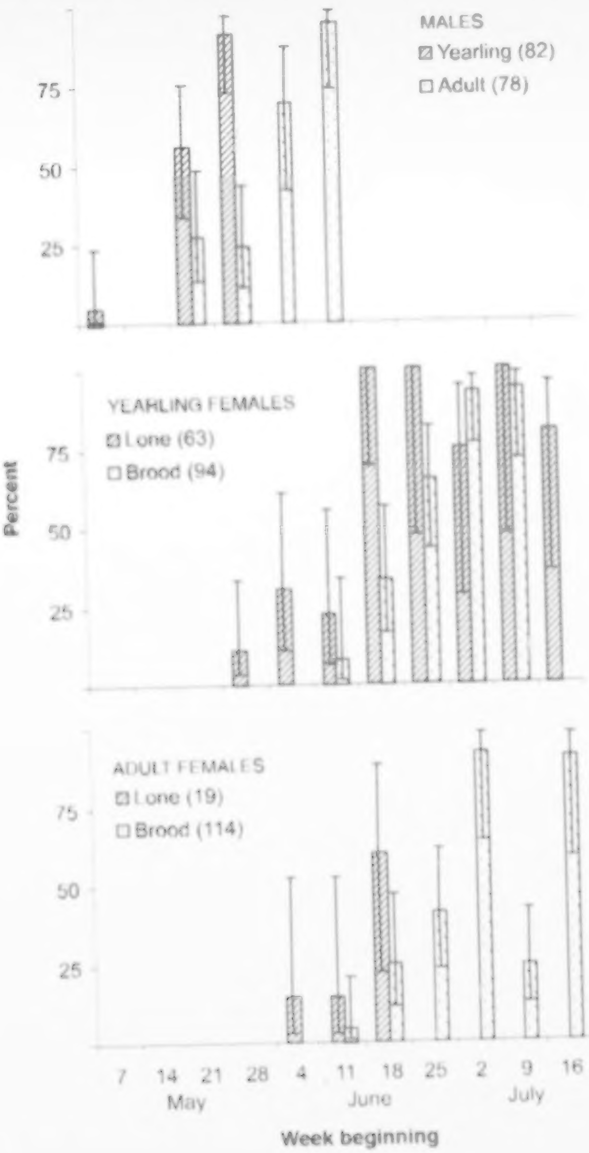


A detailed analysis of primary moult was provided for birds at Comox Burn (Zwickel and Dake 1977).[9] The earliest moult of yearling males was 13 May; adult males, 22 May; yearling broodless females, 31 May; yearling brood females, 17 June; adult broodless females, 10 June; and adult brood females, 12 June.[10]

The period in which moult began in different individuals spanned ~2 1/2 weeks in yearling males, for after 29 May all were shedding primaries. Onset in adult males spanned ~3 weeks, for after 12 June all were moulting. Initiation was earlier in yearling than adult males, but quite synchronized within age classes (Fig. 8.13). Onset also was synchronized in lone females. Among lone adults, all examined after 24 June were in moult. Among 63 lone yearlings examined after 31 May, only 2 were not moulting by 15 June—1 may have recently lost a nest, for she had an active brood patch, but the other had none. Among lone adults, all were moulting within ~2 weeks of the first, and among lone yearlings, 97% were moulting within ~2 1/2 weeks of the first.

In contrast to lone females, onset of moult of brood females spans a considerable period of time (Fig. 8.13). Other than development of the brood patch, breeding hens normally begin to moult only after termination of incubation, or of nest loss by predation or desertion (Zwickel and Dake 1977). Loss of the first primary of brood hens may occur at any time between 1 and 15 days post-hatch. At Comox Burn, all yearling brood females examined after 15 July, and all adult brood females examined after 22 July, were moulting. Onset thus spanned ~5 weeks in yearling, and ~6 weeks in adult, brood hens. The extended period in which moult of brood hens begins reflects an apparent suppression of this process during incubation. Although brood hens begin to moult last, by late August or early September, they seem to have caught up with lone hens (Zwickel and Dake 1977).

Fig. 8.13. Yearlings and adults moulting primaries (in %), by week, Comox Burn, 1969–1976. From data in Zwickel and Dake (1977).



Onset of primary moult clearly differs among sex and age classes and, especially within hens, is temporally related to breeding and incubation. Because of differences in time of breeding among and within regions, initiation dates likely differ among populations and years.

Loss and replacement of secondaries is more complicated than that of primaries and has received only cursory attention.[11] Bendell (1955*b*), on the basis of two birds, reported it was erratic. If Dwight (1900) is correct in suggesting that postnuptial moult of wing feathers follows the pattern found in replacement of juvenal secondaries, the moult of one bird described by Bendell is consistent with that described by Smith and Buss (1963), and the other is not (an aberrant bird?).

Smith and Buss found replacement of juvenal secondaries (Ss) to begin with loss of S3 and to progress proximally to S9, at which time S2 was lost (see 11.3.2(b)). Shedding continued out to S12, with S1 the last to be lost. We cannot confirm this pattern, but it is consistent with Johnsgard's (1983) suggestion that secondaries of grouse are replaced from one or two centres. If the number of secondaries is 18,[11] however, S1 may not be the last replaced.

Although we have not studied replacement of contour feathers in detail, we recorded presence or absence of moult by body regions for many necropsied birds from Vancouver and Hardwicke islands. In yearlings and adults of both sexes, contour feathers are first shed in the head and neck region, at or shortly after the first primary is lost. Among 37 yearling males, head and neck moult was first noted on 18 May, with most birds losing such feathers by 9 June. Among 95 adult males, first head and neck moult was noted on 31 May, with most birds shedding by 10 June. General body moult (head, neck, back, breast, and legs) was in progress on most adults by 20 June.

Head and neck moult was first noted in a yearling female on 16 June, among 68 birds examined. By 29 June, most yearlings, with and without broods, were losing feathers in this region, beginning as early as 14 days post-hatch in those with brood. By 20 July, most were into general body moult.

On average, body moult of adult females begins later than in yearlings, presumably because many adults, but few yearlings, have second nests (Sopuck and Zwickel 1983). Among 106 adults, head and neck moult was first recorded in a lone hen on 18 June, and in a brood hen on 2 July, the latter at <14 days after incubation ended. By 21 July, most adults with and without brood were into general body moult.

Rectrices are the last major group of feathers to be lost. Among males, 2 yearlings were replacing outer rectrices on 3 and 14 June, respectively, while 13 examined between 4 June and 3 July showed no evidence of rectrix moult (none was examined after 3 July, for most yearling males leave breeding range before replacement begins). Replacement of rectrices in two yearling males in June may have resulted from accidental loss of these feathers, and if true, tail moult in most yearling males must begin after having left breeding range.

Adult males follow a similar pattern. One that may have been losing outer rectrices was examined on 8 June. However, of 26 examined after this date, and up to 18 August, none was replacing tail feathers.[12] Within this sample, eight were collected on or after 3 July, indicating that most adult males at Comox Burn and Hardwicke Island replace rectrices after leaving breeding range. Three adult males at the Royal British Columbia Museum, collected 13 October, 23 October, and 1 November, had completed tail feather replacement.

Females, especially those with broods, stay longest on breeding range. Earliest rectrix moult in females was noted in two yearlings collected 6 and 12 July, respectively. These instances may have been caused by accidental feather loss, for not until 22 July was rectrix moult again recorded (13 were examined between 12 and 22 July). Of 10 females examined after 22 July, 8 (all in August) were replacing rectrices, with those not doing so examined on 23 and 30 July. Thus, most yearling and adult females at Comox Burn and Hardwicke Island began to replace rectrices in late July or early August. Four adult females at the Royal British Columbia Museum, collected between 6 and 16 September, were moulting tail feathers. A fifth, collected 3 October, had replaced all tail feathers. Another, collected 11 October, had lost all rectrices except the central pair. These data, along with those for males, indicate that replacement of tail feathers is more rapid and truncated than that of the primaries.

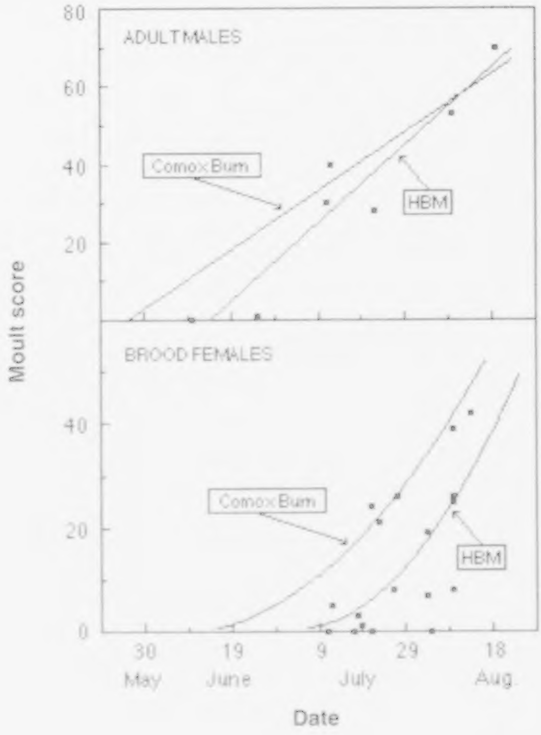
Caswell (1954*b*) was first to provide significant detail on moult of an interior subspecies, *D.o. pallidus*, in westcentral Idaho. Postnuptial moult spanned the period from late May to about October 15. He found neck moult in an adult male on 21 May, in a yearling male on 7 June, and reported that females began later than males, especially those with broods. Although Caswell was working with a relatively small sample, his results are generally consistent with our data. He suggested from birds collected in winter that some yearlings may not replace all their rectrices, but we have seen no evidence of this.

The most detailed documentation of moult of interior blue grouse is for *D.o. pallidus* in northcentral Washington (Standing 1960). Standing suggested that onset of prenuptial moult of males and females does not differ, but did not examine that of lone and brood females separately. No birds examined prior to 28 May in 1956 ($n = 27$), and 8 May in 1957 ($n = 28$), were losing primaries. No non-moulting males or females were examined after 28 May in 1956, or after 8 May (males) and 7 June (females), in 1957. Standing's Table 10 indicates that moult began with primaries and included most major feather tracts in yearlings and adults of both sexes by mid June to early July. Rectrix loss was first noted on 15 July (an adult male) but was not recorded again until 5 August (12 birds of mixed sexes and ages were examined between 16 July and 4 August). Three birds examined on or after 18 August were replacing rectrices, but completion was not documented because field seasons were terminated in August. Standing concluded that moult was initiated shortly after peak breeding and that its onset differed in the 2 years of study. Although his results are based on relatively small samples, they are generally consistent (except for brood females) with our data.

Boag (1965) described the primary moult of *D.o. richardsonii* at Sheep River. Yearling and adult males, and non-breeding females began replacement ~4 weeks prior to breeding females (mostly adults). He [rightly] questioned Standing's (1960) contention that onset of moult does not differ between males and females. Among 62 adult females examined, none began to moult prior to the end of incubation. Replacement began, on average, ~1 week after peak hatch, and these results agree closely with those from Comox Burn. The disparity between his results and those of Standing suggests Standing may not have examined any brood females. A few of our observations from other areas, in Oregon, Washington, Colorado, and Montana, also fit the patterns described for Comox Burn, suggesting a generality for them.

Another population of particular interest is at Hudson Bay Mt. Although samples are limited, onset of feather loss was clearly retarded compared to Comox Burn (Fig. 8.14) [12a, b] and parallels a late start of the breeding season there (see Fig. 10.3). It is clear in adult males, and suggested in brood females, that rate of moult is more rapid than at Comox Burn, likely an adaptation for replacing the plumage prior to onset of winter. Rate of moult was accelerated in brood females as compared to adult males, as at Comox Burn (Zwickel and Dake 1977). These data support the observation that moult is temporally related to time of breeding and that rate and onset may vary by sex, age, and within and among populations.

Fig. 8.14. Primary moult scores regressed on date for adult males and brood females at Comox Burn (Zwickel and Dake 1977) and at Hudson Bay Mt. (HBM). All data points are from HBM.



Since our field seasons usually ended in late summer, we have not documented completion of the postnuptial moult. Judging from observations of birds killed by hunters in September and October, we think it terminates in most individuals between about the middle of September and end of October in south coastal British Columbia, likely ending with complete regrowth of the outer primaries.[8,13] If true, the moulting season here spans a period of ~5 months and includes variation that is dependent on sex and breeding or non-breeding status of individuals. In alpine subalpine areas where breeding occurs at a later date, the period of moult appears to be shortened, as indicated by data from Hudson Bay Mt. Moulting spans a period when birds are either maintaining (males) or increasing (females) body mass (see 9.1(a), (b)) and when most birds are returning (migrating) to winter range (see 17.1.4), suggesting moult is not particularly stressful in blue grouse.

8.2 Bare parts

Bare parts of the integument can be separated into two types: (1) more or less featherless skin, the apteria, and (2) keratinized, horny skin, i.e., the claws, covering of the beak, and scales (scutes) on the dorsal surfaces of the toes, and the relatively softer cornified skin covering ventral surfaces of the tarsometatarsi and toes.

8.2.1 Apteria

In illustrating the pterylae of blue grouse, Clark (1899) shows locations of the apteria, and they are generally similar to those described for ruffed grouse by Bump et al. (1947).[14] In tetraonines, apteria usually occur as bare skin between, or within, the feather tracts and are normally covered by feathers originating in adjacent pterylae. Exceptions involve the lateral cervical apteria of males that may be exposed during courtship and the superciliary apteria (combs, or eyebrows), one above each upper eyelid and often exposed to view.

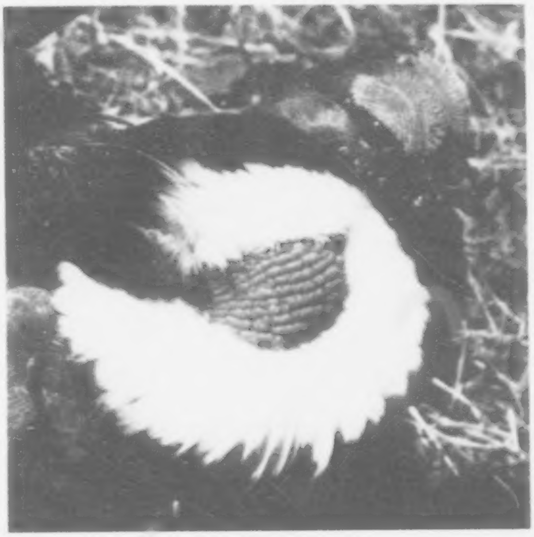
(a) *Lateral cervical apteria.* The lateral cervical apteria, one on each side of the neck, deserve individual consideration, for those of the male are highly specialized, are often exposed during display, and may be partially involved in amplification of song (Degner 1988). They are "extraordinary apteria" (in the sense of Clark 1899, p. 647) and are a sexually dimorphic secondary sex character.

These apteria of males have been referred to as rudimentary tympanums (Coues 1887), tympanums (Dawson and Bowles 1909), air sacs (Baird et al. 1874; Grinnell and Storer 1924; Bent 1932; Ridgway and Friedmann 1946), gular (Brooks 1926) and cervical air sacs (Cramp and Simmons 1980), cervical vocal sacs (Short 1967; Boag and Schroeder 1992), and gular sacs (Johnsgard 1983), all of which imply inflatable structures. Hjorth (1970, p. 265) was correct in referring to them as lateral apteria, although we prefer lateral cervical apteria (Lucas and Stettenheim 1972) because it more closely defines the area of the body on which they are found. They are highly specialized and homologous to those of male sage-grouse, sharp-tailed grouse, and prairie-chickens and to the unspecialized lateral cervical apteria of other male and female grouse. They are not sacs, but featherless skin that may appear inflatable during display, due in part to inflation of the esophagus (Degner 1988).

Lateral cervical apteria of male blue grouse in display are usually described as ". . . thick, large, tuberculate, and deep yellow in color in *fuliginosus*; not thick or tuberculate and are purplish in *obscurus* . . ." (Ridgway and Friedmann 1946, p. 68), or some variation of this quote [here, *fuliginosus* refers to all coastal, and *obscurus*, to all interior races]. In reality, those of interior males are tuberculate when in full display (Fig. 8.15, and see Fig. 41 in Hjorth (1970)), but less so than in coastal males (Fig. 8.6). In contrast to coastal birds, the tubercules are somewhat transitory in interior males and tend to regress in birds in the hand.

To the best of our knowledge, only Degner (1983) has examined the fine structure of lateral cervical apteria of any grouse in detail. He prepared histological sections from three adult males, two yearling males, three adult females, and one yearling female *D.o. fuliginosus* to compare their structures. The following descriptions are extracted, and partly modified, from his work:

Fig. 8.15. Cervical apterium of *D.o. richardsonii* in full display, Sheep River. Note the smaller tubercles than in *D.o. fuliginosus* (Fig. 8.6). Photo by SD McDonald.



Adult male—apteria are ~7 mm thick and composed of three main layers: epidermis, dermis, and a subcutaneous layer of striated muscle. The epidermis is stratified squamous epithelium, with an outer, desquamating layer that appears to be lightly keratinized. Thickness of the epidermis varies greatly (0.1–1.36 mm) and is responsible for the tuberculate appearance of the apteria. Epidermal papillae [the tubercles] may be ~2 mm tall. The dermal layer is 2–4 times thicker than the epidermis (2.2–4.4 mm) and is composed mainly of highly vascularized connective tissue. Many large to small, almost inseparable, fat globules are present in the outer half of the dermis, immediately below the epidermis. Striated muscle underlying the dermis is ~2–3 mm thick. Connective tissue and a few blood vessels are found between muscle layers. Yellow of the apteria of coastal males (approaching Buff Yellow (53)) appears to result from the large amount of fat in the outer dermis and overrides the heavy vascularization beneath [yellow may reflect carotenoid pigments within the fat].

Yearling male—apteria are similar to those of adults but with all layers thinner (total for all together is 2–3 mm). The major structural difference between age classes is that there is much less fat in yearlings, with the colour often approaching Vinaceous (3) or Flesh Color (5), not yellow as in adults. The tubercles are not as well developed, likely reflecting the lower fat content. Apteria of some yearling males appear to approach those of adults, but have not been examined histologically.

Adult and yearling females—The same layers, epidermis, dermis, and subcutaneous muscle, occur in the lateral cervical apteria, but including all together, are 7–10 times thinner than in adult males. The epidermis is 0.05–0.1 mm, the dermis, 0.1–0.4 mm, and the subcutaneous muscle, ~0.02 mm in thickness. Few blood vessels occur in the dermal connective tissue, and the amount of fat varies from almost none to a dense band that occupies most of the dermis. Apteria are approximately Flesh Color.

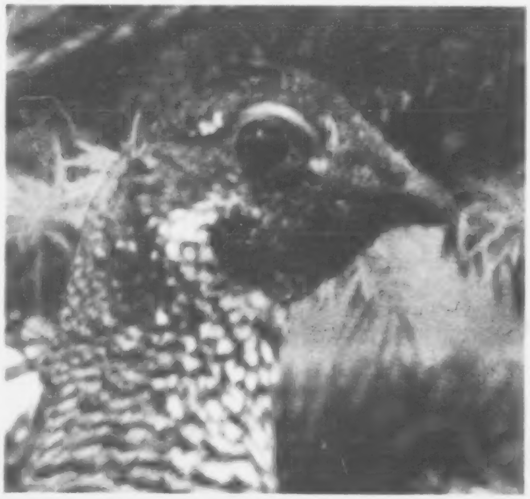
Fine structure of the lateral cervical apteria of interior males, reported as flesh coloured or raspberry (Hjorth 1970) to purple red (Bent 1932), or purplish (Ridgway and Friedmann 1946), has not been described. MA Degner (pers. comm.), however, examined histological sections of interior male apteria and says the major difference between them and those of coastal males is in the much smaller amount of fat in the dermis, making their overall structure thinner, less turgid, and, when not engorged with blood (see below), more flaccid. It seems likely the paucity of pigmented fat allows vascularization in the dermis to show through the epidermis, accounting for the more flesh-coloured appearance during display. Lateral cervical apteria of interior females are much the same as those of coastal birds (MA Degner, pers. comm.).

Degner's (1983) contention that the large amount of fat in the apteria of coastal males appears to account for their yellow colour seems true, for one can observe a more reddish colour change in the less pigmented apteria of interior males as they enter full display (pers. observ.), a change that results from flushing of the dermis with blood. This likely accounts for the somewhat transitory tuberculate nature of these apteria. Perhaps differences in their structures contribute in part to the different frequencies and (or) amplitudes of their songs (15.2.1(a)); e.g., we can envision that the thicker, more turgid, apteria of coastal males might place a different tension on the inflated esophagus (see 9.2.5(c)) and (or) syrinx than the thinner and more flaccid apteria of interior males.

It is difficult to precisely identify colour of the apteria of interior males during maximum excitement because of rapid fading in collected, or handled, specimens. We have therefore attempted to assess their colour during maximum excitement from photographs of interior males in full display (Fig. 8.15), recognizing that photographic colours may not be exactly true. We examined nine photos in which the cervical apteria most closely fall between Spinel Pink (108C) and Rose Pink (108D). Although the renditions tested may result partly from photographic colour distortion, they also may represent differing states of excitement, or individual, population, or subspecific variation. In our view, these colours are close to those found in nature. Relaxed apteria of interior males in the hand range between Flesh Color and Vinaceous, while those of interior females most closely approach Flesh Color, as in coastal females. We have seen three males at the boundary between *D.o. sierrae* and *D.o. pallidus* in which these apteria were deep orange (presumed subspecific hybrids).

Some authors have indicated, or implied, that lateral cervical apteria of coastal males are larger than those of interior males (e.g., Ridgway and Friedmann 1946; Short 1967), but these observations are largely anecdotal. This conclusion may be based on an examination of birds in the hand, in which apteria of interior males are more relaxed and shrunken than in coastal males. Photographs indicate there is little difference between coastal and interior males in full display. To test this idea, we measured maximum lengths of fully exposed apteria of coastal and interior males on a series of photos and divided this by lengths of the culmens of those birds to provide apterium/culmen ratios.[15] Since culmens of coastal and interior males are virtually identical in length (*D.o. fuliginosus*, 20.1 mm, $n = 115$; *D.o. pallidus*, 20.3 mm, $n = 16$), a large apterium will result in a larger ratio than a smaller apterium. Five coastal males had apterium/culmen ratios of 3.3, 3.3, 3.4, 3.5, and 3.6, and four interior males, 3.3, 3.6, 3.7, and 3.7. These data suggest no difference in the size of these apteria of males in full display. They are reported to partially regress outside the breeding season (Brooks 1926), but we have not examined winter specimens in this regard.

Fig. 8.16. Enlarged comb of brood female during distraction display. This is about maximum comb enlargement in females. Compare to Fig. 8.8.



(b) *Supercilliary apteria.* Males and females have "combs", above the upper eyelids. Those of males are most conspicuous and enlarge in the breeding period, representing another dimorphic secondary sex character. They are papillate and usually bright yellow (Fig. 8.4) in breeding season, but may be inconspicuous or partly concealed by feathers of the crown when birds are not sexually or agonistically stimulated (Hollett et al. 1984). Under appropriate stimulation, they are greatly enlarged, and may nearly meet on top of the crown (Brooks 1926; Hjorth 1970). In contrast to all other grouse, the colour may change rapidly, from bright yellow to orange (Fig. 8.6), to bright red under peak stimulation, owing to flushing with blood (Blackford 1958; Hjorth 1970; Hollett et al. 1984; pers. observ.).[16] Combs of females are less conspicuous (Fig. 8.8), are often concealed under feathers of the crown, and were described as "dull orange–yellow" by Ridgway and Friedmann (1946, p. 72), a description with which we concur. They may slightly enlarge (Fig. 8.16) under appropriate circumstances, especially in females with broods. Those of aviary females appear smaller and less conspicuous in winter than summer, but we have not examined wild birds in this regard.

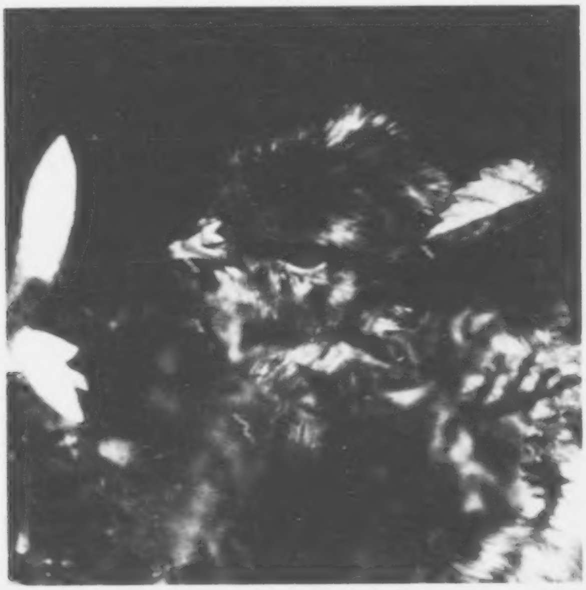
8.2.2 Beak and feet

(a) *Beak.* The beak is covered by keratinized horn. Blackish in mature males, it may vary from blackish to dark brown in mature females, to grayish brown or dark brown in juveniles, to medium or light brown in small downy young.

Birds have a horny tubercle at the tip of the upper mandible in the maturing embryo, the egg-tooth (Fig. 8.17). The fully developed embryo uses the egg-tooth to cut the eggshell at time of hatching (Van Tyne and Berger 1966). In blue grouse it is cast off shortly after hatching, in the first day of life.

(b) *Feet.* The dorsal and lateral surfaces of the tarsometatarsi are feathered, but the ventral surfaces are bare. The epidermis has not been examined histologically but appears externally as a mosaic of minute keratinized polygons (each < 1 mm across).

Fig. 8.17. Day-old chick with egg-tooth on tip of the beak. Photo by J Kristensen.



The reticulate nature of this cornified skin makes it somewhat pliable, though held closely to the bone by connective tissue. The same epidermal structure is found on the plantar surfaces of the feet and toes but is more pliable and padlike, apparently a result of cushioning by a greater amount of connective tissue.

Dorsal and lateral surfaces of the toes are scutellate, covered with a single row of overlapping, horny scales, with free ends distal. These wrap dorsally over the digits from one side to the other. Exposed surfaces of the scales are ~1.5 mm wide in females and ~2 mm wide in males, in a posterior-anterior sense. Ridgway and Friedmann (1946) describe the feet of males as light brownish gray and the claws as blackish brown, the feet of females as pale brownish gray to pale greenish gray, with the soles and backs of the tarsometatarsi yellowish and claws pale horn gray.

A single row of cuticular pectinations, so-called "snowshoes", are found on each side of the toes in winter. They occur at the junction between the lateral edges of the digital scutes and the plantar digital pads. These growths are usually ≤2 mm long in birds we have examined, very small incomparison to those of some of the other grouse, especially since blue grouse are heavy bodied birds. For example, pectinations of ruffed grouse, about one-half the size of blue grouse are usually ~2 mm long (New York State) and are reported to be longer in more northern areas (Edminster 1947). We have seen museum specimens of ruffed grouse in which pectinations were up to 3 mm in length, and of sharp-tailed grouse in which they were up to 5 mm in length. It seems strange that a bird as heavy bodied as blue grouse and that often winters in areas of heavy snowfall would have such small pectinations when compared to much smaller tetraonines. Perhaps this is an adaptation to their largely arboreal lifestyle in winter.

8.3 Synthesis

As a major organ system, the integument of birds contributes to a number of bodily functions, including (among others) thermoregulation, protection against mechanical injury, and, through its most distinctive attribute, plumage, the ability to fly.

Along with behavioural attributes discussed in Chap. 15, different subspecies of blue grouse have been described principally on the basis of colouration of the plumage and numbers of rectrices. The sexually dimorphic plumage of this bird contributes, in males, to elaborate courtship displays, and in females, to cryptic colouration important to survival and completion of the reproductive cycle.

Chicks hatch with a covering of natal down and acquire two other plumages in their first 14 weeks of life, juvenal and postjuvenal. A postnuptial moult is repeated at annual intervals throughout the remainder of an individual's life and involves a complete, or near complete, change of plumage each year.

Hens that breed (perhaps some that don't) shed all or most feathers in the abdominal region to form a brood patch, a seasonal apterium of incubating females. This loss of feathers is accompanied by fatty oedema and vascularization of the skin, presumably adaptations for maintaining proper temperatures and humidity for developing embryos. Development and refeathering of the brood patch varies with time of nesting, within and among populations.

The postnuptial moult begins with shedding of the first primary, likely ends with complete regrowth of P10, and is temporally linked to the breeding cycle. Yearling and adult males moult first, followed by non-breeding, or unsuccessful breeding, females, then females with broods. Late onset in brood females appears adaptive, since nesting females lose body mass during incubation, and moulting at this time might contribute to undue stress. Moult appears to end in most populations in late September or October, but the specific time needs better documentation.

Onset of the postnuptial moult varies among populations. In those with late breeding the rate appears to be accelerated when compared to those that breed earlier. This ensures that all birds complete their annual moult prior to onset of winter. Both sexes generally maintain or gain mass and migrate to winter range while moulting.

As with North American prairie grouse, the lateral cervical apteria of males are highly specialized and used in courtship, a character unique among non-lekking tetraonines. Both sexes have superciliary apteria, "combs", with those of males largest and which greatly enlarge in the breeding season, especially during sexual and agonistic interactions. Epidermal covering of the beak and feet is featherless. Winter pectinations on the toes, so-called "snowshoes", are relatively small when compared to other tetraonines.

Endnotes [Chapter 8]

1. We use Smithe (1975) to identify some colours. They are identified by capitalized name (and number) when first introduced, but there is variation within and among populations and subspecies. Colours undergo subtle seasonal changes as plumage fades or

becomes worn, so specific colours can be used only as a general guide.

2. We follow Lucas and Stettenheim (1972) in naming pterylae and apteria.

3. This characteristic was described for *D.o. fuliginosus*, but general observations indicate it holds for other subspecies, though intensities of colours may vary. It is best developed on the most posterior upper tail coverts.

4. We used only yearlings and adults for this analysis because juveniles are less easily assigned to race.

5. Three birds with distinct tail bands may have been misclassified as to race, transients from coastal regions, or subspecific hybrids (Zwickel et al. 1991).

6. Unfortunately, our examination was cursory, and our notes provide no further detail. This specimen deserves a closer examination.

7. We once proposed that presence of a brood patch is indicative of nesting (Zwickel and Bendell 1967). Lance (1967), however, identified a brood patch on a radio-marked hen that was not known to mate or nest and questioned its utility as a criterion for breeding. We have now documented brood patches on three of five radio-marked yearling hens at Comox Burn for which no nests were found. This is not proof a brood patch can develop without breeding, for nests of those with brood patches may have been missed. Nests have been found, however, for 19 of 20 radio-marked adult hens at various study areas, with the sole exception, a hen killed by a predator, apparently during laying. This suggests we find virtually all nests of radio-marked hens. Standing (1960) found yearling females with well-developed brood patches whose ovaries indicated little or no evidence of having ovulated. The question as to whether a brood patch is a valid criterion of breeding remains open.

8. Hens that nest, including those that renest, usually do not begin to replace feathers in the brood patch until termination of incubation. A female at Middle Quinsam that sat through two incubation periods on dead eggs, however, provides an exception, for after 52 days, feather replacement was ~50% complete. A second female, a yearling with 4-day-old chicks, had new feathers in her brood patch with >0.5 cm vanes on 28 July; almost certainly a hen that renested.

9. Study of primary replacement is especially useful because in most birds it spans the entire period of moult (Snow 1967; Seel 1976), which seems true in blue grouse.

10. Dates for yearling brood females and lone and adult brood females are slightly later than reported by Zwickel and Dake (1977) owing to the inclusion of new data and larger sample sizes.

11. The number of secondaries in blue grouse is subject to interpretation. Clark (1899) suggested 18, but it is difficult to determine where (on the elbow) they end. Bendell (1955*b*) and Smith and Buss (1963) indicate 12. Secondaries are counted beginning distally at the wrist, at which point they are clearly separable from primaries. In blue grouse this feather tract extends proximally around the elbow onto the brachium (humerus). Feathers on the elbow and brachium are sometimes considered as tertiaries and in some species clearly differ from secondaries of the antebrachium (Pettingill 1946), but this is not clear in blue grouse. We counted these feathers closely in three juveniles and two adults and found 14 between the wrist and elbow joint in all cases (perhaps 15, for the break is not clear), and four beyond the elbow joint in four birds, five in the fifth (teriaries?). We suggest the usual number is 14 or 18, depending on the terminology one follows.

12. Apparent rectrix moult in the male examined 8 June may represent accidental loss of outer tail feathers.

13. Three adult males at the Royal British Columbia Museum collected 13 October, 23 October, and 1 November, and one adult female collected 3 October, had completed their primary moult; another adult female collected 11 October had replaced all primaries but P10.

14. Note, however, Clark seems to have made one major oversight because he considered blue grouse as having no "extraordinary apteria" on the neck.

15. Only birds in full display and lateral view were measured.

16. Combs of male spruce grouse are highly vascularized. An increase in capillary density in the breeding season "facilitates enlargement of the comb during sexual and agonistic encounters" (Hollett et al. 1984, p. 193). This appears true in blue grouse.

CHAPTER 9

Morphology

Descriptive anatomy, well done, does not become obsolete.

AM Lucas and PR Stettenheim (1972)

We have not done anatomical studies *per se* but have examined and measured selected external and internal components of many blue grouse. Some are more or less stable seasonally, while others vary, providing possible insights into evolutionary and ecological relationships. When possible, e.g., in the case of body mass, we compare to data from other studies. We consider morphological studies of the syringes and esophagi principally from the work of Degner (1983, 1988).

9.1 Body size

Blue grouse are seventh largest among the tetraonines, exceeded only by capercaillie, sage-grouse, and most populations of black grouse, in descending order of size.[1] Blue grouse show strong sexual size dimorphism, approximately the same as that of black grouse (Zwickel et al. 1966) and are exceeded only by capercaillie and sage-grouse.

9.1.1 Body mass

Body mass is perhaps the most widely used index to size and condition but may vary among areas, seasons, years, age classes, individuals, and between sexes. Seasonal variation may relate to breeding, migration, nutrition, and moult; annual variation, to weather, population density, nutrition, and variations among age classes (Redfield 1973*c*). Mass is labile, and it is important to recognize factors that may affect its use as an index to size or condition.

(a) *Spring and summer patterns on Vancouver Island.* A number of workers have examined mass of yearlings and adults (Bendell 1955*b*; Boag 1965; Zwickel et al. 1966; Redfield 1973*c*; Harju 1974; Schladweiler 1974, among others). Bendell provided the first seasonal analysis, for birds at Lower Quinsam (Table 9.1). He reported no significant change in the mass of adult males among the periods April–May, June–July, and September. We computed a grand spring–summer mean of 1250 g for these birds from his data. Mean mass of eight yearling males from May and June was significantly less than that of adult males. Spring mass of females was not examined because of the rapid changes going on in that season, and the mean for adults in June–July (Table 9.1) was essentially the same as that of adult females shot by hunters in September.

Redfield (1973*c*) provided more comprehensive analyses of body masses for birds in the Ash River area. His major conclusions, spanning April to early September, were that (1) mean mass of yearling and adult males did not change seasonally, and (2) mean mass of yearling and adult females changed seasonally. Mass of females increased from April to May, decreased sharply during incubation, and was minimum in June. Maximum mass was at 30–40 days prior to hatch (the approximate time of egg-laying) with a minimum at or about time of hatch. Redfield's graphs suggest a slight, but likely insignificant, upward trend in masses of yearlings and adults from June to September. Those of yearling males and females were always less than in adults of the respective sexes, and there were significant differences among years in all sex and age classes, but with no consistency among groups. He was unable to explain the latter differences, and we suspect they were a result of relatively small yearly sample sizes.

The largest spring and summer sample of body masses of yearlings and adults is from Comox Burn (Fig. 9.1). There was a significant difference among monthly means of adult males, but no difference when masses from August were excluded [1a, b]. We think the difference among all months results from the very small sample in August ($n = 6$). If so, there was little, or no, change from April to August, consistent with the Lower Quinsam and Ash River data. The grand mean for adult males for the period April to July, 1273 ± 4 g ($n = 482$), is very similar to, and likely not significantly different from, a grand spring–summer mean of ~1280 g for those at Ash River (computed by us from Redfield's Table 1, $n = 116$).

As at Ash River, monthly masses of yearling males at Comox Burn (Fig. 9.1) did not differ significantly [2]. A grand mean for all months combined, 1112 ± 5 g ($n = 237$), is identical to that of ~1112 g for birds at Ash River (computed by us from Redfield's Table 2, $n = 129$).

Yearling and adult females at Comox Burn followed a seasonal pattern similar to that reported for females at Ash River. In both age classes, mass increased significantly from April, to a maximum in May (Fig. 9.1) [3a, b].[2] Mass of broodless females in both age classes declined significantly from May to June and June to July, when many hens were incubating eggs, but not from July to August [3a–f].[3]

Minimum masses attained by yearling and adult females were those of brood females in June (Fig. 9.1), immediately

Table 9.1. Body masses (g, mean ± SE) of yearling and adult blue grouse in various parts of their range. Except where noted, masses include crop contents.

	Males		Females	
	Yearling	Adult	Yearling	Adult
LOWER QUINSAM (*D.o. fuliginosus*)[a]				
April–May		1285±30 (21)		
May–June	1110±40 (8)			
June–July		1230±10 (34)	790±10 (11)	845±10 (55)
September		1245±50 (6)		850±10 (37)
CA, OR, WA (*D.o. sierrae*)[b]				
Spring–summer		1218±21 (19)		
SE WYOMING (*D.o. obscurus*)[c]				
Spring	1039 (15)	1168 (26)	830 (4)	910 (5)
Summer			767 (9)	786 (19)
Autumn		1094 (33)		844 (10)
SKALKAHO (*D.o. pallidus*)[d]				
Spring–summer	1101±35 (9)	1271±10 (29)		
Post-incubation			718±17 (4)	830±12 (19)
MONTANA (*D.o. pallidus*)[e]				
Spring–summer	1118 (57)	1281 (209)		
1 July–15 August			800 (41)	833 (120)
METHOW VALLEY (*D.o. pallidus*)[f]				
Spring–summer	1002±31 (3)	1171±13 (41)		
July–August			810±9 (23)	855±8 (64)
NORTHCENTRAL WASHINGTON (*D.o. pallidus*)[g]				
Autumn				
Chumstick	1069±32 (11)	1136±10 (76)	830±36 (21)	875±7 (63)
Conconully	1157±18 (27)	1212±5 (246)	872±7 (74)	905±4 (252)
SHEEP RIVER (*D.o. richardsonii*)[h]				
Spring–summer		1217±10 (68)		
May–June	1004±20 (20)			
July, post-incubation			813±8 (49)	
July–August			831±16 (26)	

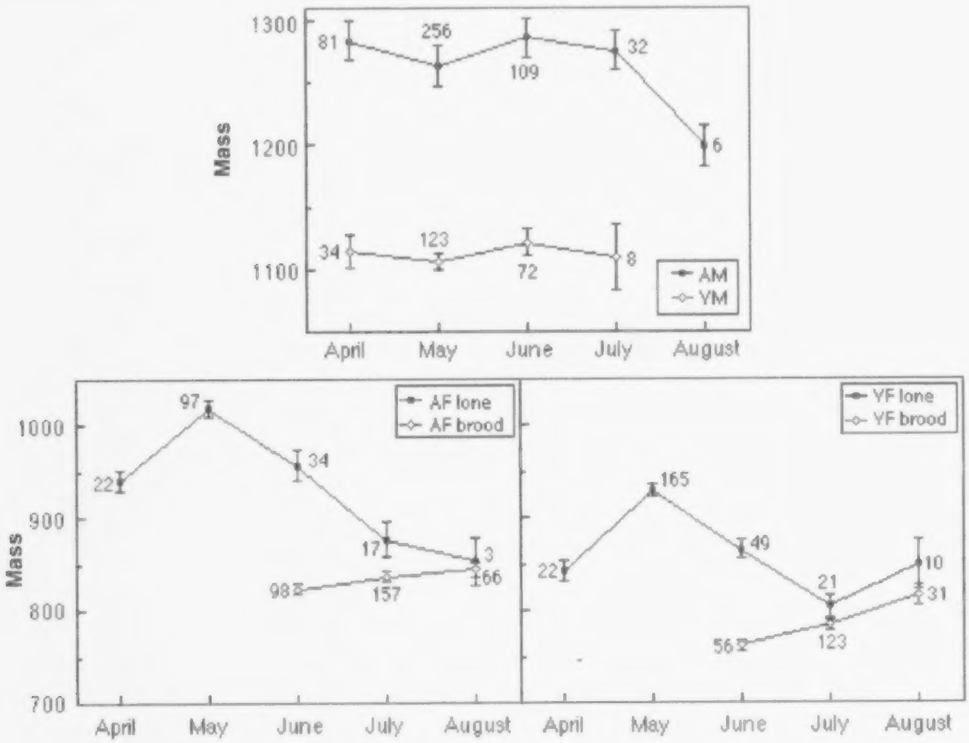
[a] Data from Bendell (1955*b*); crop contents excluded.
[b] Data from this study; combined samples from California, Oregon, and Washington.
[c] Data from Harju (1974).
[d] Data from this study, 1986.
[e] Compiled from data in Table 6 of Schladweiler (1974); combined samples from several study areas and years.
[f] Combined samples collected by Standing (1960), Henderson (1960), Bauer (1962), Degner (1988), and this study.
[g] Data from Zwickel et al. (1966); adults include some unrecognizable yearlings.
[h] Data from DA Boag.

post-incubation or when with very small chicks. Mean minima of yearlings and adults were 18% (167 g) and 19% (197 g) less than mean maxima (in May) for each age class, respectively. These percentages are minimal because mean maxima include some birds that have completed portions of incubation, by which time they would have lost some mass. Mean masses of yearling brood females increased significantly each month, June to August [4a, b]. Those of adults were not significantly different from June to July or July to August but showed a steady upward trend, and were different between June and August [4c–e].

Body masses of birds from subalpine areas adjacent to Comox Burn tended to be less than birds from the lowlands (King 1971). King suggested that subalpine birds may take 3–4 years to attain maximum adult mass, or might represent a different genotype than lowland grouse.

We also weighed birds shot by hunters at our checking station near Courtenay, from 1970 to 1979. This station was operated on the last weekend in August or first weekend in September each year. Mean masses of yearling and adult males, data for all years combined, were 1177 ± 28 g (n = 9), and 1244 ± 11 g (n = 41), respectively. The sample for year-

Fig. 9.1. Mean monthly body masses (g ± SE) of yearlings and adults at Comox Burn, 1969–1977. Sample sizes are shown.



lings is small but suggests an increase over the spring–summer mean of 1112 g.[4] That for adults was less than the spring–summer mean for this age class but was likely lowered by the inclusion of some yearlings that had completed their postnuptial primary moult and were classified as adults. We suspect no loss in mass of adult males at this time.

Mean masses of yearling and adult females shot by hunters, data for all years combined, were 829 ± 6 g (*n* = 122), and 863 ± 3 g (*n* = 339), respectively. Brood and broodless females were combined in these samples, so these data cannot be compared directly to those for August at Comox Burn (Fig. 9.1). Nevertheless, it appears they would be very similar to combined means for these two reproductive classes in August, within respective age classes.

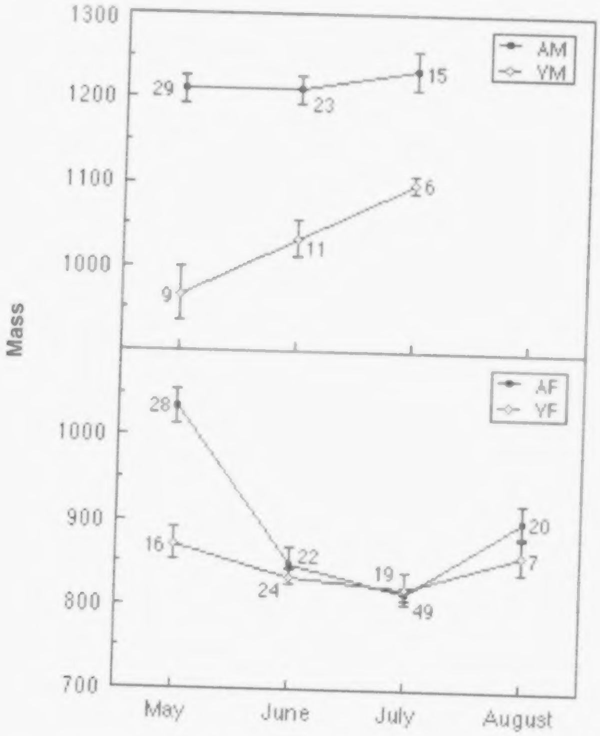
Bendell's (1955*b*) grand mean of 1250 g for adult males at Lower Quinsam was ~25–30 g less than for birds at Ash River and Comox Burn. Bendell, however, excluded crop contents from his analyses, and were this not done, his mean for adult males likely would not be different from those of birds at these areas. His May–June mean of 1110 g for a small sample of yearling males (crop contents excluded) was essentially the same as the 1112 g mean for yearling males at Ash River and Comox Burn. Except that his adult females showed no gain in the post-hatch period,[5] his data are in agreement with those for Ash River and Comox Burn.

We conclude for all three lowland populations of grouse from central Vancouver Island: (1) there is little, or no, seasonal change in spring–summer monthly mean body masses of yearling or adult males, and (2) there is a marked seasonal change in monthly mean body masses of yearling and adult females. The latter includes a spring increase after arriving on breeding range, a peak during egg-laying, a rapid loss during incubation, and a slow recovery over summer. By late summer, females have not attained their previous spring mass, indicating further recovery takes place in autumn, winter, or early spring. Broodless females weigh more than brood hens in the post-hatch period, likely because they have not bred or completed incubation (thus avoiding the loss that accompanies incubation).[6] Lastly, yearlings weigh less than adults in both sexes, confirming suggestions of Bendell (1955*b*), Boag (1965), Zwickel et al. (1966), and Redfield (1973*c*) that birds do not attain adult mass in their second summer.

(b) *Spring and summer patterns at Sheep River*. Seasonal body masses of grouse at Sheep River show some clear similarities and differences when compared to those on Vancouver Island. Studies there (unpublished data from DA Boag) encompassed May to August, so comparisons with April could not be made (most birds were apparently still on winter range in much of April (DA Boag, pers. comm.)). As well, brood and broodless females often were not identified as such, so these groups were combined.

Mean monthly body masses of adult males (Fig. 9.2) did not differ significantly in spring and summer [5], as with birds on Vancouver Island. Mean masses of yearling males differed among months [6a]. That in May was not different than in

Fig. 9.2. Mean monthly body masses (g ± SE) of yearlings and adults at Sheep River, 1955–1966. Data courtesy of DA Boag. Sample sizes are shown.



June, which was not different than in July, but May and July differed [6b]. There was a clear upward trend over this period, a sharp contrast to yearling males on Vancouver Island, suggesting significant growth. Mean masses in May and June were significantly less than the grand mean for yearling males at Comox Burn, 1112 g, but that for July was not [7]. Males at Sheep River appear to not attain full yearling mass until midsummer of their second year of life, ~4 months later than on Vancouver Island.

Mass of adult females (Fig. 9.2) indicated a seasonal pattern similar to that at Ash River and Comox Burn. It peaked in May, with a sharp and significant drop in June[7] [8a]. It did not change significantly from June to July, but the mean for these months combined, 824 ± 9 g (n = 71), was significantly less than in August [8b]. Adult females here clearly recovered mass after completing incubation, perhaps more rapidly than on Vancouver Island.

In contrast to birds on Vancouver Island, mass of yearling females (Fig. 9.2) did not differ among the months May to August [9]. The relatively low mass of yearlings in May helps to explain Boag's (1966) report that few yearlings in this population breed. Most may be physiologically unable to breed, perhaps because of inadequate body reserves to carry them through incubation. Some do breed, however, and the downward trend from May to July, although statistically insignificant, may indicate a loss of mass. Relatively low masses of yearling males and females in May suggest a slower rate of growth for these birds in their first summer and (or) winter than for birds on Vancouver Island. This may reflect the later hatch and earlier onset of winter there, a shorter first-year season of growth.

(c) *Mass in winter*. There are few data on winter body masses, too few from which to extract firm conclusions. Some suggestions are possible, however.

Standing (1960) compared mean masses in February and March to those in spring and summer for birds in the Methow Valley. He concluded that adult males are heaviest just prior to onset of breeding and gradually lose mass throughout spring and summer. He presented no monthly sample sizes or measures of variation, however, making his interpretations difficult to substantiate. In examining his Fig. 47, we suspect there is little, or no, loss in adult males through spring and summer, with his suggestion of peak mass in late winter subject to error caused by small monthly samples. Standing also concluded that masses of adult and yearling females increased in spring, up to time of laying, decreased into June, and levelled off or increased through summer. In all cases but one, individuals in August were lighter than, or approximately equal to, females at time of arrival on spring range (March or April), suggesting mass is gained between autumn and spring, when birds are on winter range. Some anomalies in his graphs likely reflect small samples, and his conclusions must be viewed with caution.

Data from Comox Burn support the proposal that blue grouse gain mass in winter. For example, that of adult males in September (which may include some yearlings) was less than that of adult males in spring, as also was true for yearling and adult females (Fig. 9.1). Yearling males, too, weigh less in autumn than adult males in spring, the age class to which they advance. Bendell's (1955*b*) data for adult males at Lower Quinsam and Harju's data for adult males and females from southeast Wyoming (Table 9.1) are consistent with this conclusion.

(d) *Range in mass of the sex and age classes*. Although mean body masses of yearling and adult males and of yearling and adult females are significantly different, there is considerable overlap of ranges within sexes (Table 9.2). Such overlap extends to comparisons between sexes and within other populations. Peak mass of females, however, tends to be short-lived and to represent females in early spring, when fully gravid. Minimum mass of females tends to be that of hens with broods, birds that have recently completed incubation. Mass at, or near, either end of the range is usually represented by

Table 9.2. Range in body mass (g) of yearlings and adults at Comox Burn and in hunting samples from that region. Sample sizes are in parentheses.

	Yearling	Adult
COMOX BURN		
Spring–summer males	900–1390 (238)	1020–1500 (482)
Broodless females	690–1090 (267)	750–1180 (173)
Females with brood	650–1000 (210)	700–1000 (321)
HUNTING SAMPLES (autumn)		
Males	1040–1300 (9)	1080–1380 (41)
Females	600–1000 (122)	700–1033 (339)

only one or a few individuals. Minima might be from ill or abnormally small individuals. Although 1500 g is the maximum mass recorded for any blue grouse on Vancouver Island, one heavier bird has been identified, a 1575-g adult male at Hardwicke Island. This was clearly an abnormally large bird and the heaviest blue grouse documented to date.

(e) *Mass dimorphism between sexes*. Males are clearly heavier than females. Since female mass is seasonally labile and that of males relatively constant, however, the proportional difference varies seasonally. For example, at Comox Burn, adult females in May, at seasonal maximum, are approximately 80% as heavy as adult males, but when with brood in June, only 65% as heavy. In July, brood and broodless adult females are 66% and 69%, respectively, as heavy as adult males. The pattern for yearlings is similar, but with mass of females 3%–5% closer to that of males in respective categories,[8] likely reflecting fewer breeding females in yearlings than in adults.

Since there is strong seasonal variation in mass of females in the breeding season, autumn provides the least biased period in which to examine mass dimorphism.[9] Mean autumn masses of adult females at Chumstick and Conconully were 77% and 75% those of adult males in the two areas (Zwickel et al. 1966). That of adult females in southeast Wyoming also was 77% that of adult males (means in Table 9.1). Autumn samples from Vancouver Island suggest mass dimorphism there might be greater than in northcentral Washington and southeast Wyoming, for adult females at Lower Quinsam were 68%, and those at Courtenay, 69%, as heavy as adult males. Data were gathered earlier on Vancouver Island (late August or early September), however, than in the other areas (mid September, or later), giving these females less time to recover from post-hatch lows. As well, females may recover faster in interior than coastal populations, but this is speculative. We conclude that the mean autumn mass of females is 70%–75% that of males, similar to that of black grouse (75%) in Finland (Koskimies 1958).

(f) *Comparisons among populations and subspecies*. Body mass may vary among populations, or perhaps, subspecies. Judging from analyses of seasonal patterns on Vancouver Island and at Sheep River, adult males show little variation in spring and summer. We therefore use combined spring–summer masses of adult males as an index to examine differences among populations and subspecies.

Table 9.3. Spring–summer body masses (g) of adult males at Comox Burn, CA–OR–WA, Skalkaho (1986), Sheep River, and the Methow Valley.

Area	*n*	Mean ± SE	Range
Comox Burn	482	1273±3.7	1020–1500
CA–OR–WA	19	1217±21.0	1096–1460
Skalkaho (1986)	86	1271±10.5	1180–1405
Methow Valley	41	1170±13.0	1020–1338
Sheep River	68	1217±10.2	1021–1403

Note: Birds from Comox Burn, *D.o. fuliginosus*; Skalkaho and Methow Valley, *D.o. pallidus*; CA–OR–WA, *D.o. sierrae*; and Sheep River, *D.o. richardsonii*.

Data are available that allow statistical comparisons among five populations (Table 9.3). Mean masses of adult males at Comox Burn and Skalkaho were not different [10a], and these represent the largest birds among populations compared. Adult males at Comox Burn and Skalkaho were heavier than those from Sheep River, CA–OR–WA, and the Methow Valley [10b–g]. Males from Sheep River and CA–OR–WA were not different, but both were heavier than those from the Methow Valley [11a–c]. Thus, adult males from Comox Burn and Skalkaho (*D.o. pallidus*) were heaviest, with those from the Methow Valley (also *D.o. pallidus*) lightest. Males from CA–OR–WA (*D.o. sierrae*) and Sheep River (*D.o. richardsonii*) were approximately the same; intermediate between the other groups. Mean mass appears to reflect local populations as much as subspecific variation. Although we could not make statistical comparisons to these groups, male *D.o. obscurus* from southeast Wyoming (Table 9.1) appear to be relatively small, while those from several Montana study areas (*D.o. pallidus*) were essentially the same as at Skalkaho in 1986.

It is difficult to make comparisons among females from different populations,[10] but some general observations may be made from Table 9.1 and Figs. 9.1 and 9.2. During periods that were clearly post-incubation for most females, i.e. between 1 July and 31 August, mean masses of yearling females ranked among areas approximately as follows: Sheep River > Lower Quinsam = Comox Burn = Methow Valley = Montana > southeast Wyoming. Four birds from Skalkaho (1986) showed the lowest mean, but this may reflect the small sample. The relatively high mean for yearlings from Sheep River may reflect a low rate of breeding by these birds (Boag 1966), i.e., most had not experienced incubation and its attendant loss. Post-incubation masses of adult females ranked among areas approximately as follows: Lower Quinsam = Comox Burn = Sheep River > Methow Valley > Montana = Skalkaho (1986) > southeast Wyoming. Females from Vancouver Island stand out as relatively heavy birds and those from southeast Wyoming as relatively light birds, consistent with trends shown by adult males. Sheep River and Methow Valley females appeared heavier, and Montana females lighter, than might be predicted from adult males, but these data may be affected by time of breeding and (or) varying post-hatch recovery of mass in the different areas.

Another set of data also suggests differences among populations but within subspecies, that from birds shot by hunters and examined at Chumstick and Conconully (Table 9.1). In all four sex and age classes, birds at Conconully were significantly heavier than at Chumstick (Zwickel et al. 1966), even though both represent *D.o pallidus* and the areas are only ~120 km apart.

9.1.2 Other external morphometrics

External measurements other than body mass are sometimes used as indices to overall size or to examine size of particular body components. These measurements provide comparisons among sex and age classes that may be preferable to mass because of seasonal variations in the latter. In other cases, they may complement data on mass or be used in conjunction with them as an index to condition.

Table 9.4. External body measurements (mm, mean ± SE) and mass (g, mean ± SE) of yearling and adult males and females, coastal British Columbia.

	Mean length (mm ± SE)		Yearling as
	Yearling	Adult	% of adult
MALE			
Total length	475±2.1 (39)	501±2.1 (109)	95
Wing[a]	222±0.6 (121)	229±0.4 (263)	97
Tail	151±1.7 (41)	169±1.1 (119)	89
Culmen	21±0.4 (42)	20±0.2 (115)	105
Foot[b]	98±0.2 (336)	99±0.2 (333)	99
Tibiotarsus	95±1.3 (34)	96±0.8 (87)	99
Middle toe	58±0.8 (47)	59±0.3 (124)	98
Middle claw	12±0.4 (45)	12±0.2 (124)	100
Body mass[c]	1177±28 (9)	1244±11 (41)	95
FEMALE			
Total length	442±2.1 (79)	448±1.5 (117)	99
Wing[a]	204±0.3 (350)	208±0.3 (358)	98
Tail	131±1.0 (75)	138±0.7 (114)	95
Culmen	19±0.2 (75)	18±0.2 (108)	106
Foot[b]	90±0.1 (670)	91±0.2 (413)	99
Tibiotarsus	87±0.9 (61)	88±0.7 (99)	99
Middle toe	54±0.4 (81)	54±0.3 (120)	100
Middle claw	11±0.2 (85)	11±0.2 (127)	100
Body mass[c]	829±6 (122)	863±3 (339)	96

Note: Body, wing, tail, and culmen were measured as in Anderson (1965); wing with primaries flattened. Foot was measured as for chicks (see Endnote 7, Chap. 11); tibiotarsi from the junction of the tibiotarsus and femur to the junction of the tibiotarsus and tarsometatarsus; middle toe along its upper surface from proximal to distal ends, excluding the claw; claw from upper junction with the middle toe to its tip. Except where noted, data are from Comox Burn and Hardwicke Island combined. Sample sizes are in parentheses.

[a] Data from Hardwicke Island only.

[b] Data from Comox Burn only.

[c] Mean autumn body masses of grouse shot by hunters and examined at Courtenay (see text).

We examined relatively large numbers of collected birds at Comox Burn (mainly) and Hardwicke Island and recorded foot and wing (Hardwicke Island only) lengths on birds captured and released in banding studies. We use these data to examine other external body parameters.[11]

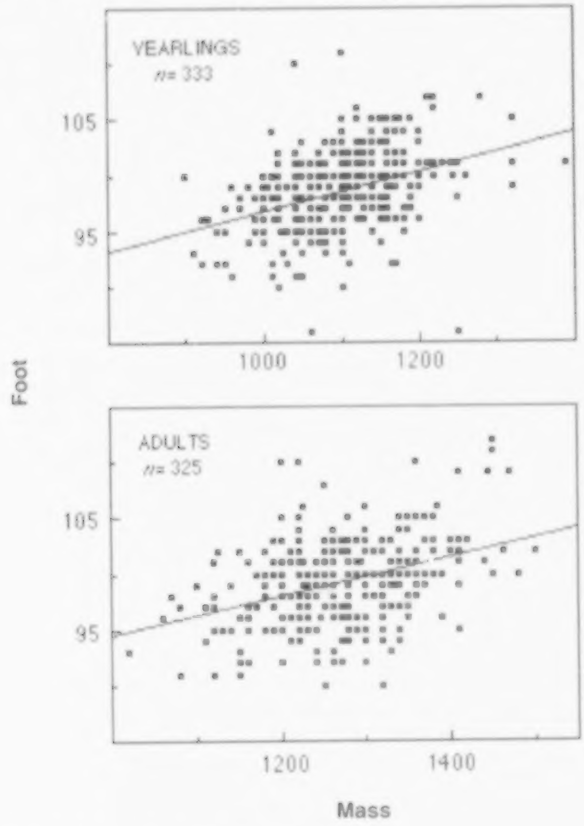
In all external measurements (Table 9.4) but one, within age classes, males were significantly larger than females [12a]. The exception was length of the middle claw of yearlings [12b], perhaps a statistical anomaly.

Within sexes, mean lengths of body (total length), wing, tail, and foot were all significantly larger in adults than yearlings. Culmens were longer in yearlings than adults [13a–j], which may reflect greater wear on those of adults than in yearlings, though this is speculative. In neither sex was there a significant difference in lengths of tibiotarsi, middle toes, or middle claws between yearlings and adults [13k–p]. In most respects, yearlings had not attained adult size, but in the case of the culmen and measurements associated with the lower legs and feet, they had.

We examined size relationships between age classes for measurements that differed significantly by expressing yearling measurements as a percent of those of adults. In all instances except tail length in males, yearling measurements were ≥95% those of adults (Table 9.4). In some cases, e.g., foot in both sexes, yearling means were ~99% those of adults. In general, means based mainly on bone, e.g., tibiotarsus and middle toe, were not different between yearlings and adults, or only slightly different, e.g., foot. Those involving a plumage component, i.e., body length, wing, and tail, suggest greater differences. Body mass, too, suggests a greater difference between age classes than components involving mainly bone. Thus, skeletal measurements may be the best index to body size, but unfortunately, no detailed studies of the skeleton of blue grouse, or most of its parts, are available. Overall, yearling females tended to be closer to adult size than were yearling males. In this respect yearling females appear more mature than yearling males.

How do linear body measurements relate to mass? As judged by data from Comox Burn, there was a significant positive relationship between length of foot and body mass in yearling and adult males (Fig. 9.3) [14a, b], but with a large amount of variation. Data from Hardwicke Island indicate a similar, and significant, positive relationship between length of wing and body mass in yearling and adult males (Fig. 9.4) [15a, b], but again, with a large amount of variation.

Fig. 9.3. Relationship between body mass (g) and length of foot (mm) of yearling and adult males, Comox Burn, 1969–1978.



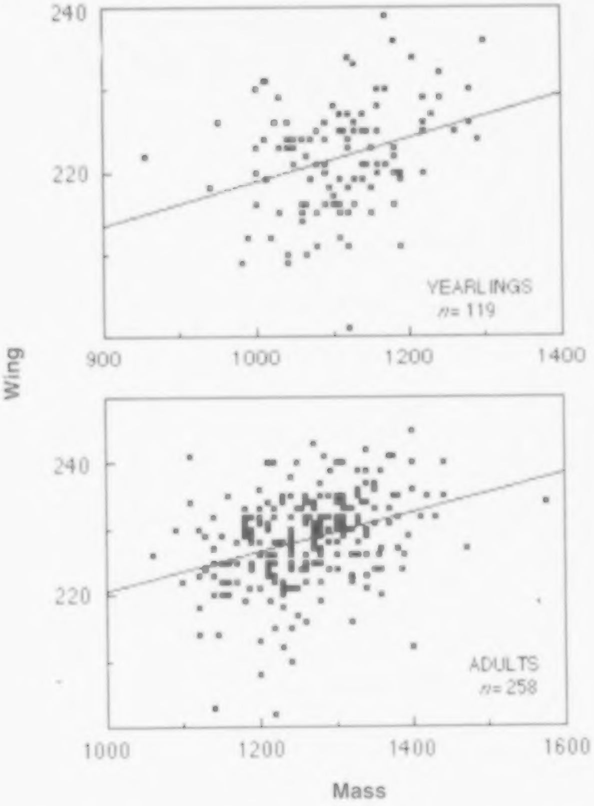
9.2 Internal morphometrics

The two major breast muscles, *M. pectoralis major* and *M. pectoralis minor*, and major internal organs were weighed or measured during necropsies of most collected birds from Comox Burn and Hardwicke Island.[12,13]

9.2.1 Yearling and adult males

Yearling males (Table 9.5) showed the least seasonal variation of all sex and age classes. There were no differences among monthly means for either of the major breast muscles or for any organs [16a] except the gizzard. Mean mass of the gizzard was not different among the months May to July, but a combined mean for these months was less than for April [16b]. The change from maximum mass in April to that from May to July was 9.3 g, a loss of 28%. High gizzard mass in April likely reflects that birds had just come off winter range where the diet is largely composed of coniferous needles, a highly fibrous food.[14] Once on spring–summer range, broad-leaved herbs, berries, and other less fibrous foods are added to the diet and this likely accounted for the decline at this time. Mass of the gizzard lining was not different among months [17], with a spring–summer mean of 3.7 ± 0.1 g ($n = 44$). This represented 11% of the mass of the gizzard (with lining) in April and 15% of the mass in May to July, suggesting spring–summer loss is mainly muscle tissue.

Fig. 9.4. Relationship between body mass (g) and length of wing (mm) of yearling and adult males, Hardwicke Island, 1979–1984.



Combined mean mass of the *pectoralis majors* and *pectoralis minors*, 312 g (Table 9.5), accounted for 28% of spring–summer body mass (1112 g) of yearling males. These muscles are clearly the largest single contributor to body mass. The small amount of seasonal variation in these muscles and most internal organs is consistent with the constant spring–summer body mass of yearling males.

Adult males, too, showed little seasonal change among internal body parts, though more than in yearlings. There were no seasonal differences in monthly mean masses of the *pectoralis major*, *pectoralis minor*, heart, liver, or pancreas, or in mean lengths of the small intestine, or ceca (Table 9.6) [18a]. The proventriculus [18b, c] and spleen [18d, e] differed among months or periods, and the colon was longer in April than other months. There were no differences among other months [18f].

The gizzard, heaviest in April, declined significantly in May–June and appeared to recover slightly in July–August [19a, b]. The change from maximum in April to a May–June minimum was 9.6 g, a loss of 28%, identical to that of yearling males. As in yearlings, this likely reflected a change in diet. The gizzard lining of adult males showed no seasonal change [20], with a spring–summer mean of 4.0 ± 0.1 g ($n = 112$) and represented 11% of gizzard mass (with lining) at its maximum, in April, and 16% of mass at its minimum, in May–June. Monthly differences in masses of the proventriculus and spleen do not seem to fit a clear pattern, and we can offer no

Table 9.5. Masses of major breast muscles and selected internal organs (g) and lengths of selected internal organs (mm) of yearling males.

Body component	Period[a]	*n*	Mean ± SE
MASS			
Pectoralis major	Spring–summer[b]	38	236.9±3.4
Pectoralis minor	Spring–summer	38	74.9±1.0
Heart	Spring–summer	41	6.3±0.2
Gizzard	April	3	33.3±0.6
	May–July	41	24.0±0.6
Proventriculus	Spring–summer	42	4.0±0.1
Liver	Spring–summer	43	24.0±0.6
Spleen	Spring–summer	32	1.3±0.1
Pancreas	Spring–summer	20	2.5±0.2
LENGTH			
Small intestine	Spring–summer	41	1391±18.9
Colon	Spring–summer	42	139±3.5
Cecum (1 only)	Spring–summer	41	531±6.0

Note: Data are from birds collected at Comox Burn and Hardwicke Island combined.

[a] Data for contiguous monthly means not significantly different are combined. Only two birds in July and none from August.

[b] Spring–summer: mean for the period from April to July, as there was no difference among monthly means; no yearling males were sampled in August.

Table 9.6. Masses of major breast muscles and selected internal organs (g) and lengths of selected internal organs (mm) of adult males.

Body component	Period[a]	*n*	Mean ± SE
MASS			
Pectoralis major	Spring–summer[b]	94	255.3±2.3
Pectoralis minor	Spring–summer	94	78.5±0.7
Heart	Spring–summer	109	6.3±0.2
Gizzard	April	13	34.8±1.5
	May–June	89	25.2±0.4
	July–August	10	28.7±1.1
Proventriculus	April–May	54	3.8±0.1
	June	45	4.3±0.2
	July–August	11	3.5±0.2
Liver	Spring–summer	109	22.7±0.5
Spleen	April	11	2.1±0.4
	May	30	1.1±0.1
	June–August	39	1.4±0.1
Pancreas	Spring–summer	49	2.1±0.1
LENGTH			
Small intestine	Spring–summer	108	1419±10.7
Colon	April	96	145±1.8
Cecum (1 only)	Spring–summer	109	551±5.1

Note: Data are from birds collected at Comox Burn and Hardwicke Island combined.

[a] Data for contiguous monthly means not significantly different are combined. Only three birds from August.

[b] Spring–summer: mean for April to July, as there was no difference among monthly means.

explanation for them. Note, though, they are small organs that contribute little to total mass.

Combined mass of the *pectoralis majors* and *pectoralis minors*, 334 g (Table 9.6), accounted for 26% of the mean April to July body mass (1273 g) of adult males, similar to that of yearlings (28%). As in yearlings, small seasonal variation in these muscles and the major internal organs is consistent with a relatively constant spring–summer body mass.

9.2.2 Yearling and adult females

There was greater seasonal variation in internal body components of females than in males. Much of this parallels, and helps explain, changes in body mass of females in spring and summer. Note, however, that necropsy samples include both brood and broodless females and that samples from May and June, especially, included females in various stages of incubation, a period in which total mass decreases markedly.

Some body components of yearling females showed no significant changes in spring–summer. These included the *pectoralis minor*, proventriculus, spleen, pancreas, and small intestine (Table 9.7) [21a]. Perhaps the heart and ceca also should be included in this category, for both indicated seasonal changes between spring–most of summer and August [21b, c], but with the August sample from only two birds. Differences may have been an anomaly of this small sample.

Components that showed seasonal variation included the *pectoralis major*, gizzard, liver, and colon. All were heavier, or longer (colon), in April–May than from June to August, with no differences within these periods [21d–g]. This generally parallelled seasonal changes in body mass associated with nesting, incubation, and raising of young. Changes in the gizzard and colon, especially, may be associated mainly with a seasonal shift in diet, from relatively fibrous (high proportion of conifer needles) to less fibrous foods (see Fig. 12.4). The change from maximum gizzard mass in April–May to a minimum in June to August, a loss of 1.6 g (7%) is much less than the 28% found in yearling and adult males. The gizzard lining, too, showed a significant difference in mass between April–May, 3.4 ± 0.1 g ($n = 35$), and June to August, 2.9 ± 0.1 g ($n = 40$) [21h], a contrast to the situation in males. The lining constituted 15% and 14% of gizzard mass (with lining) in each period, respectively.

Combined mass of the *pectoralis majors* and *pectoralis minors* of yearlings when at mean maximum, 243 g (Table 9.7), accounted for 26% of the mean maximum body mass in May (929 g). Combined mass of these muscles at their minimum, 221 g, accounted for 29% of the mean minimum body mass of brood females (762 g, in June). These muscles thus constituted a relatively constant percentage of total mass of yearling females in spring–summer, a percentage comparable to that found in yearling (28%) and adult (26%) males. A decrease of 21.8 g between the maximum and minimum represents a 9% loss, one-half the difference between maximum and minimum body masses (18%). However, minimum muscle masses included brood and broodless females, so the 9% difference is minimal and not directly comparable to that for body mass, which was from brood females only.

Table 9.7. Masses of major breast muscles and selected internal organs (g) and lengths of selected internal organs (mm) of yearling females.

Body component	Period[a]	*n*	Mean ± SE
MASS			
Pectoralis major	April–May	27	187.7±5.3
	June–August	33	165.9±3.4
Pectoralis minor	Spring–summer[b]	60	54.9±0.9
Heart	May–July[c]	2	4.3±0.1
	August	2	6.1±0.6
Gizzard	April–May	35	22.6±0.6
	June–August	41	21.0±0.4
Proventriculus	Spring–summer	71	3.3±0.1
Liver	April–May	29	25.6±1.1
Spleen	Spring–summer	60	1.2±0.1
Pancreas	April–May	29	2.8±0.6
	June–August	19	1.7±0.1
LENGTH			
Small intestine	Spring–summer	71	1330±17.3
Colon	May[c]	33	146±2.4
	June–August	40	127±2.8
Cecum (1 only)	April–July	71	491±5.5
	August	2	389±1.5

Note: Data are from Comox Burn and Hardwicke Island combined.

[a] Data for contiguous monthly means not significantly different are combined. Only one bird was examined from April, a bird collected 25 April, and only two from August.

[b] Spring–summer: mean for April to August, as there was no difference among monthly means.

[c] No sample from April.

Adult females showed the greatest seasonal variation in internal body components of the four sex and age classes. The proventriculus and small intestine were the only structures that did not change (Table 9.8) [22a].

Most internal body components of adult females were heaviest, or longest, in April (heart, gizzard, colon), April–May (*pectoralis major*, liver, pancreas), or April to June (*pectoralis minor*), and lightest, or shortest, in June (colon), July (*pectoralis minor*, heart), June–July (gizzard), July–August (*pectoralis major*, ceca), or June to August (liver, pancreas) [22b–i]. There is a suggestion that some of these structures were increasing by August (*pectoralis minor*, heart, gizzard) or July–August (colon), but only four birds were examined in August (Table 9.8). An increase is consistent with the upward trend in body mass of adult females at that time. The general pattern of all components was maximum size in spring, minimum in early to midsummer (following incubation), with some recovery in late summer. The only exception to this was the spleen, which was significantly larger in July–August than April to June [22j] and for which we have no explanation. Perhaps blood parasites were involved, but we have no information on this point.

The pattern of change in the gizzard of adult females was essentially the same as in yearling and adult males; maximum in April, a large decrease by May, and no, or smaller, changes in June and July. The decrease from a maximum in April to a minimum in June–July was 9.7 g, a loss of 31%, similar to the 28% loss in yearling and adult males, but more than four times that of yearling females (7%). As in yearling females, the gizzard lining showed significant seasonal change; heaviest in April–May, 3.8 ± 0.1 g ($n = 46$), and lightest from June to August, 3.0 ± 0.1 g ($n = 61$) [22k]. The lining constituted 12% and 14% of the mass of the gizzard (with lining) during each period, respectively. A decline in the lining of females but not males may reflect more herbaceous foods taken by females in spring and summer (see 12.1.2(a), (b)).

Table 9.8. Masses of major breast muscles and selected internal organs (g) and lengths of selected internal organs (mm) of adult females.

Body component	Period[a]	*n*	Mean ± SE
MASS			
Pectoralis major	April–May	44	217.1±3.2
	June	17	195.4±4.7
	July–August	43	178.3±2.6
Pectoralis minor	April–June	62	62.8±0.9
	July	39	57.9±1.1
	August	4	61.7±2.3
Heart	April	16	5.5±0.2
	May–June	48	4.8±0.1
	July	43	4.1±0.1
	August	3	4.9±0.6
Gizzard	April	16	30.8±0.9
	May	31	23.7±0.7
	June–July	59	21.1±0.4
	August	4	25.9±2.4
Proventriculus	Spring–summer[b]	107	3.5±0.1
Liver	April–May	40	24.4±0.9
	June–August	63	17.6±0.5
Spleen	April–June	56	0.8±0.0
	July–August	35	1.1±0.1
Pancreas	April–May	40	2.3±0.1
	June–August	15	1.5±0.1
LENGTH			
Small intestine	Spring–summer	105	1324±11.6
Colon	April	15	157±3.9
	May	32	143±3.3
	June	16	124±4.3
	July–August	46	135±3.1
Cecum (1 only)	April	16	530±15.6
	May	31	492±6.5
	June	17	515±14.9
	July–August	45	458±6.9

Note: Data are from birds collected at Comox Burn and Hardwicke Island combined.

[a] Data for contiguous monthly means not significantly different are combined. Only four birds from August.

[b] Spring–summer: mean for April to August, as there was no difference among monthly means.

Seasonal change of *pectoralis majors* of adult females was similar to that in yearlings. This was not true for *pectoralis* *minors*, for that of adults changed, while that of yearlings did not. The difference between age classes may relate to having larger samples of adults, i.e., there was a better chance of detecting a difference, especially since that between maximum and minimum masses was relatively small in adults (8%). An alternative explanation is that the difference reflected that most adults breed, thus undergoing incubation, while some yearlings may not breed (Hannon and Zwickel 1979; Zwickel 1980). Since these samples include brood and broodless females, a small seasonal change that might occur in brood hens could be masked by the inclusion of more non-breeders in the yearling sample.

Combined *pectoralis majors* and *pectoralis minors* when at their maxima, 280 g (Table 9.8), accounted for 27% of the maximum body mass of adult females (1020 g, in May at Comox Burn). Combined mass when at their minima, 236 g, accounted for 29% of the mean minimum body mass of brood females (823 g, in June). As in yearlings, these muscles constitute a relatively constant percentage of the total mass of adult females in spring–summer, a percentage similar to that of yearling (28%) and adult (26%) males. A decrease of 43.7 g between maximum and minimum masses of these muscles (combined) represents a 16% difference, a little less than that between maximum and minimum monthly body masses (19%). This is considerably higher than the 9% found in yearling females and may be explained, at least in part, by the inclusion of some non-breeders among yearlings. Since most mass is lost during incubation, more renesting in adults than in yearlings (Sopuck and Zwickel 1983) also may contribute to the difference between age classes.

9.2.3 Morphometrics in other populations

We compared body masses among populations above (9.1.1) and have other measurements of grouse from various areas. The larger samples are from adult males, so we use mainly these for comparative purposes.

(a) *Length of foot*. Feet of adult males at Hudson Bay Mt. were significantly larger than in any other population (Table 9.9) [23a–e]. Those of males from Hardwicke Island (the same as at Comox Burn) and Skalkaho did not differ [24a], but both had larger feet than males from CA–OR–WA, the Methow Valley, and Hart's Pass [24b–g], with no differences among the latter populations [24h]. Thus, adult males from Hudson Bay Mt., a "hybrid" subalpine population, had large feet, those from Hardwicke Island, a coastal population, and Skalkaho, an interior population, had relatively large, similar-sized feet, and those from CA–OR–WA, a coastal race, and the Methow Valley, the same race as at Skalkaho, and from "hybrids" at Hart's pass, had similar-sized, small feet. Adult males from CA–OR–WA are largely arboreal in breeding season, while *D.o. pallidus* from the Methow Valley and Skalkaho are largely terrestrial. These data suggest no clear relationship between size of foot, breeding habitat (see Chap. 7), use of breeding habitat, or subspecies.

Since there appears to be a relationship between size of foot and body mass of adult males within populations (Fig. 9.3), we examined this relationship among populations. Mass was significantly correlated with length of foot among populations (Fig. 9.5) [25]. If one assumes birds in all populations were in relatively similar condition, size of foot appears to be a fair predictor of body size.

(b) *Length of wing*. Adult males from Skalkaho had the longest wings (Table 9.9), significantly longer than in any other population sampled [26a–e]. Wings of males from the Methow Valley were next longest and longer than those of all other populations except Hudson Bay Mt., from which they did not differ [27a–d]. Since Methow Valley birds are small (Table 9.1) and Hudson Bay Mt. birds large (Fig. 9.5), the relative wing length of Methow Valley birds is greater than that of birds at Hudson Bay Mt. Wings of males from Hardwicke Island were shorter than those of males from CA–OR–WA and Hudson Bay Mt., but did not differ from those at Hart's Pass [28a–c]. Thus, Hart's pass "hybrid" and Hardwicke males had

Table 9.9. Lengths (mm ± SE) of foot and wing of adult males among populations.

Population	Mean length	
	Foot	Wing
Hardwicke Island (*D.o. fuliginosus*)	100.2±0.2 (257)	228.5±0.4 (263)
CA–OR–WA[a] (*D.o. sierrae*)	94.6±0.6 (20)	231.9±0.9 (20)
Methow Valley, WA (*D.o. pallidus*)	94.2±0.8 (16)	236.2±1.6 (16)
Skalkaho (1986) (*D.o. pallidus*)	99.2±0.5 (27)	239.9±0.8 (27)
Hart's Pass, WA (*D.o. fuliginosus* × *D.o. pallidus*)[b]	93.0±1.3 (9)	230.9±1.8 (9)
Hudson Bay Mt. (*D.o. fuliginosus* × *D.o. richardsonii*)[b]	102.2±0.8 (13)	232.4±1.7 (13)

Note: Sample sizes are in parentheses.

[a] Combined sample from northeastern California, southcentral Oregon, and southcentral Washington.

[b] Presumed subspecific hybrid population.

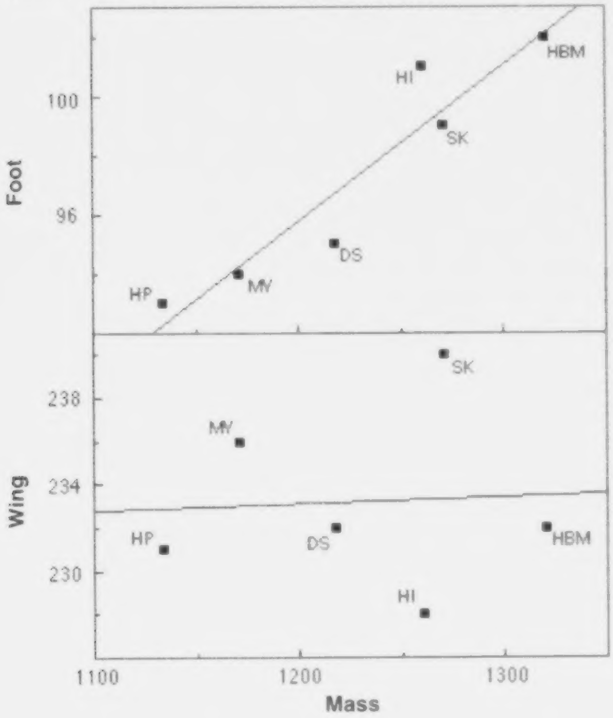


Fig. 9.5. Relationship between mean body mass (g) and mean length of foot (mm) and wing (mm) of adult males from Hart's Pass (HP), the Methow Valley (MV), Skalkaho (SK), Hardwicke Island (HI), Hudson Bay Mt. (HBM), and combined *D.o. sierrae* from California, Oregon, and Washington (DS). See text for subspecific designations.

relatively short wings. Hudson Bay Mt. "hybrid" and CA–OR–WA birds had longer wings, and Methow Valley and Skalkaho males, the longest wings. There is thus a correlation between the long wings of *D.o. pallidus* (Methow Valley and Skalkaho), their use of relatively open habitats, and a mostly terrestrial lifestyle in breeding season when compared to shorter winged coastal males, their use of more forested habitat, and a more arboreal lifestyle in breeding season. Males of both hybrid populations were relatively short-winged and strongly arboreal in breeding season.

As with length of foot, there appeared to be a positive relationship between body mass and length of wing within the Hardwicke Island population (Fig. 9.4). In contrast to the foot, however, there was no relationship between length of wing and body mass among populations (Fig. 9.5) [29]. This suggests some factor other than body size has had an effect on length of the wing, perhaps something associated with kinds of habitat in which the birds evolved. Perhaps longer wings of interior males are associated with the more complex, terrestrial flutter flights of these birds, as compared to the less complex, usually arboreal flutter flights of coastal birds (see 15.2.3(f)). Females do not perform flutter flights, however, and wings of adult (215 ± 1.3 mm, $n = 25$) and yearling (211 ± 1.6 mm, $n = 13$) females at Skalkaho were significantly longer than those of females at Hardwicke Island (adults, 208 ± 0.3 mm, $n = 358$; yearlings, 204 ± 0.3, $n = 350$) [30a, b]. Thus, male and female *D.o. pallidus* have longer wings than *D.o. fuliginosus*, suggesting the difference in males may not be related to display behaviour. Foot lengths of females at the two areas were in the opposite direction: adult females at Skalkaho, 90 ± 0.6 mm ($n = 25$), at Hardwicke, 92 ± 0.2 mm ($n = 338$); yearling females, at Skalkaho, 90 ± 0.6 mm ($n = 13$), at Hardwicke, 92 ± 0.2 mm ($n = 331$). Adults were significantly different between areas, yearlings nearly so [30c, d].

(c) *Other organs and body components.* We have limited necropsy samples from three areas that allow us to compare other external and internal body components of adult males to those from Vancouver and Hardwicke islands. For reference, we include body masses of birds included in the necropsy samples from the four areas (Table 9.10), of which, birds at Hart's Pass have not been considered before. Recall that body mass of *D.o. fuliginosus* > *D.o. sierrae* > Methow Valley *D.o. pallidus*, and that, among all populations and subspecies, *D.o. fuliginosus* were heavy birds, and Methow Valley *D.o. pallidus*, light birds. Those from Hart's Pass weighed significantly less than those from Vancouver–Hardwicke islands and CA–OR–WA but were not different from those from the Methow Valley (Table 9.10), indicating that they too are low-mass birds [31a–c].

There were no differences in body or culmen lengths (Table 9.10) among these samples [32a, b]. Tails of males from Vancouver and Hardwicke islands were shorter than in any other group, which did not differ among themselves [33a–d]. Tibiotarsi of males from Vancouver–Hardwicke islands were longer than those at Hart's Pass and nearly longer than those of birds from CA–OR–WA and the Methow Valley [34a–c]. The latter three did not differ among themselves [34d]. Middle toes of males from Vancouver–Hardwicke islands were longer than in any other population, which did not differ among themselves [35a–d]. Length of the middle claw did not differ among the four groups [36]. Males from Vancouver–Hardwicke islands stand out as heavy birds with short tails, short wings, long tibiotarsi, and large feet.

Pectoralis majors of males at Vancouver–Hardwicke islands were significantly heavier than those of males in any other sample. Those of CA–OR–WA birds did not differ from Methow Valley birds but were greater than those from Hart's Pass, which did not differ from Methow Valley males [37a–f]. *Pectoralis minors* also were heaviest in birds from Vancouver–Hardwicke islands, with those of CA–OR–WA and Methow Valley males not different. Both were heavier than in Hart's Pass birds [38a–f]. Owing to their large contributions to body mass, these muscles undoubtedly are major contributors to differences in total mass among populations.

Hearts were heavier in males from Vancouver–Hardwicke islands than in other populations, which did not differ among themselves [39a–d]. Livers of birds from Vancouver–Hardwicke islands were heavier than those of CA–OR–WA birds, with no differences among the other populations [40a, b]. The above components generally parallel total body masses of the different populations, and a failure to do so precisely is likely related to the relatively small samples of CA–OR–WA, Methow Valley, and Hart's pass birds. Spleens of CA–OR–WA males were heavier than in populations from Vancouver and Hardwicke islands and the Methow Valley, and nearly so at Hart's Pass. Others did not differ among themselves [41a–d].

Table 9.10. Body size components (mean ± SE) of adult males among populations.

	Vancouver–Hardwicke islands[a]	CA–OR–WA[b]	Methow Valley[c]	Hart's Pass[d]
EXTERNAL				
Body mass (g)	1274±7 (119)	1218±21 (19)	1171±13 (41)	1134±24 (9)
Lengths (mm)				
Body	501±2.1 (109)	500±5.9 (20)	512±3.6 (16)	495±4.7 (9)
Tail	169±1.1 (119)	178±2.5 (20)	184±2.8 (16)	182±2.8 (9)
Culmen	20±0.2 (115)	20±0.4 (20)	20±0.5 (16)	20±0.4 (9)
Tibiotarsus	96±0.8 (87)	91±1.2 (20)	92±1.2 (16)	90±2.0 (9)
Middle toe	59±0.3 (124)	55±0.7 (18)	54±1.2 (16)	53±1.3 (9)
Middle claw	12±0.2 (124)	13±0.4 (20)	14±0.8 (16)	12±0.9 (9)
INTERNAL				
Mass (g)				
Pectoralis major	255±2.3 (94)	238±4.2 (20)	225±6.9 (8)	211±9.6 (9)
Pectoralis minor	79±0.7 (94)	72±1.9 (20)	72±1.7 (8)	63±3.3 (9)
Heart	6±0.2 (109)	6±0.1 (18)	5±0.4 (11)	5±0.3 (8)
Gizzard	25±0.4 (89)[e]	32±1.1 (20)	25±0.8 (12)	31±0.9 (9)
Proventriculus	4±0.1 (54)[f]	3±0.2 (19)	4±0.3 (12)	3±0.1 (8)
Liver	23±0.5 (109)	19±0.8 (19)	22±1.1 (9)	21±1.1 (8)
Spleen	1±0.1 (30)[g]	2±0.4 (11)	1±0.1 (10)	1±0.5 (7)
Lengths (mm)				
Small intestine	1419±11 (108)	1235±34 (18)	1352±58 (11)	1181±42 (8)
Colon	145±1.8 (96)[h]	156±2.8 (18)	150±4.3 (11)	152±5.7 (9)
Cecum (1 only)	551±5.1 (109)	493±12.4 (18)	505±26.0 (11)	499±15.4 (9)

Note: All data are from necropsy samples. Sample sizes are in parentheses.

[a] *D.o. fuliginosus.*

[b] *D.o. sierrae.*

[c] *D.o. pallidus.*

[d] *D.o. fuliginosus × D.o. pallidus* "hybrids".

[e] Data for May to June only because of seasonal variation (Table 9.6).

[f] Data for April to May only because of seasonal variation (Table 9.6).

[g] Data for May only because of seasonal variation (Table 9.6).

[h] Data for May to August only because of seasonal variation (Table 9.6).

Samples of spleens were relatively small, which may account for some apparent differences, or lack of differences, among populations.

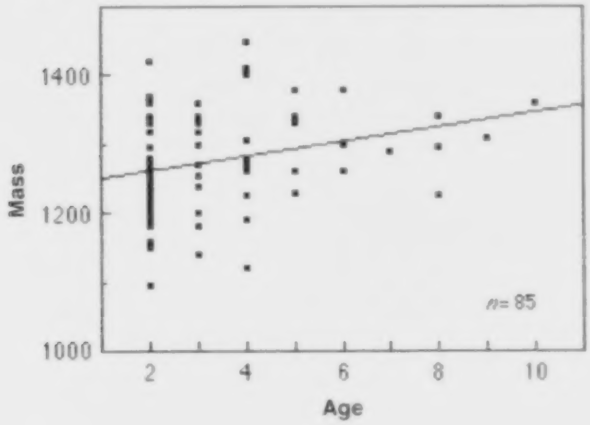
Masses of gizzards and proventriculi did not parallel body masses and appear more related to food habits than to body size. For example, masses of gizzards of Vancouver–Hardwicke islands and Methow Valley males were not different but were significantly smaller than those of CA–OR–WA and Hart's Pass males, which did not differ [42a–f]. Adult males in the former samples were largely terrestrial in breeding season,[15] those in the latter, largely arboreal, with the former having a large component of broad-leaved herbs in the spring–summer diet and the latter feeding mainly on conifer needles. Larger gizzards of CA–OR–WA and Hart's Pass males correlate with a more fibrous diet. In contrast, proventriculi of Vancouver–Hardwicke islands and Methow Valley males did not differ, but both were heavier than in birds from CA–OR–WA and Hart's Pass [43a–e]. This organ, too, may vary with diet, but in the opposite direction to that of the gizzard.

Length of the small intestine of males from Vancouver–Hardwicke islands was significantly longer than those of males at CA–OR–WA and Hart's Pass and nearly longer than those from the Methow Valley, with no difference among the latter populations [44a–d], although they approached significance. Length of the ceca of males from Vancouver–Hardwicke islands was longer than that of any of the other groups, which did not differ among themselves [45a–d]. Mean lengths of colons did not differ among any samples [46]. Birds at Vancouver and Hardwicke islands thus appear to have long guts relative to the other populations.

9.2.4 Body size and increasing age

Blue grouse of both sexes, on average, are heavier and larger as adults than as yearlings. This is a long-lived species, and one can ask, do body mass or other components of size change beyond age 2? Since mass of adult males shows little change in spring–summer, we used this sex and age class to examine this question.

Fig. 9.6. Body masses (g) of known-aged (in years) males, Comox Burn, 1969–1978, and Hardwicke Island, 1979–1984. Data for areas combined.



Body masses of 85 known-aged males ranging from 2 to 10 years old (data from Comox Burn and Hardwicke Island) showed a significant tendency to increase with age (Fig. 9.6) [47], but with a large overlap in individual masses among year classes. The increasing tendency could result from either increased mass with age, or a survival advantage for heavier males. Thirty-seven banded males were captured and weighed in different years, with time between captures ranging from 1 to 7 years. Twenty-five weighed more, three the same, and nine less at second capture as compared to when first caught.[16] Numbers weighing more and those weighing less were significantly different than the 1:1 ratio expected if there were no change with age [48]. These data suggest a tendency for body mass of adult males to increase with age. Whether adult females show the same tendency cannot be examined because of limited samples and seasonal lability in their mass.

The foot of adult males also tended to increase with age (Fig. 9.7) [49a], although there was again much overlap among year classes. The foot of known-aged females did not show the same trend, i.e., no increase with age [49b]. These data, along with those on mass, indicate that males tend to increase in size with age, but females do not.

9.2.5 Miscellany

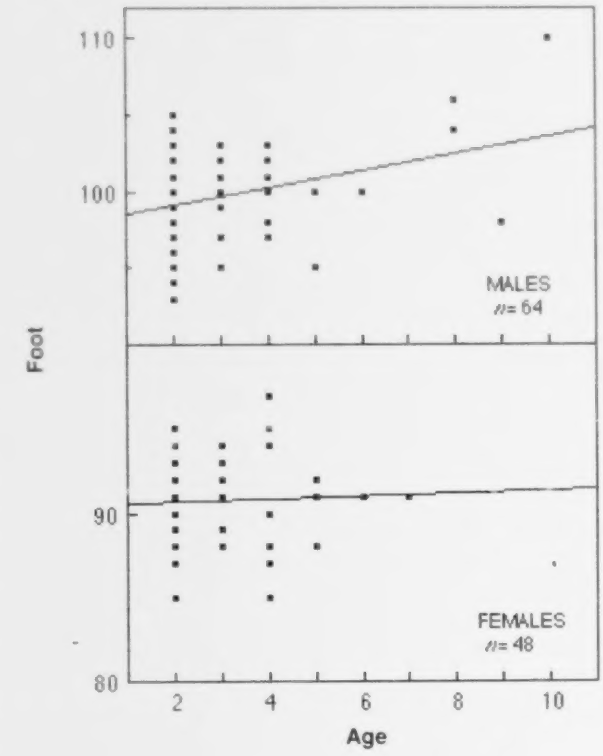
(a) *Skeletal measurements*. We measured lengths of femurs, sternums, and maximum depth of the keel of sternums of a small sample of necropsied birds from Comox Burn and Hardwicke Island (Table 9.11). Lengths of sternums and femurs of adult males were significantly longer than in yearling males, and depths of keels were almost different [50a–c]. There were no differences in any of these measurements between adult and yearling females [50d–f]. Within age classes, all were significantly greater in males than females [51a–f]. Although samples were small, these data suggest these skeletal elements of yearling males had not fully matured (in terms of size), while those of yearling females had.

Table 9.11. Lengths (mm, mean ± SE) of femurs, sternums, and depths of keels of yearling and adult males and females from Vancouver and Hardwicke islands.

	Femur	Sternum	Keel
Yearling male	74.3±0.47 (9)	92.3±0.86 (9)	34.0±0.47 (9)
Adult male	75.8±0.41 (12)	96.0±1.13 (10)	35.5±0.65 (10)
Yearling female	67.7±0.74 (5)	84.2±1.49 (5)	30.8±0.75 (5)
Adult female	67.6±0.69 (4)	87.3±1.45 (5)	30.5±1.14 (5)

Note: Sample sizes are in parentheses.

Fig. 9.7. Length of foot (mm) of known-aged (in years) adult males and females, Comox Burn, 1969–1978, and Hardwicke Island (males only), 1979–1984. Data for areas combined.



(b) *The syringes and esophagus: relationships to song*. Although the lateral cervical apteria have, by implication, been proposed as song-producing organs in males, it is now generally accepted that song is produced in the syrinx (Bendell and Elliott 1967; Hjorth 1970). In shape and size, the syrinx of male blue grouse appears to be the largest and most complex of all North American tetraonines (pers. observ.). As well, males possess an inflatable esophagus that may act as a resonating chamber for sounds produced in the syrinx (Degner 1988). Taken together, these characters may account for the very low frequency of the song of blue grouse (see15.2.1(a)).[17]

Syringes of blue grouse are strongly sexually dimorphic (Fig. 9.8). Those of both sexes are composed of all the essential components of a "simple syrinx"—cartilaginous syringeal rings separated by connective tissue, a pessulus, internal, and perhaps, external, tympanic membranes, two pairs of muscles,

Fig. 9.8. Syringes of males and females—from left to right: ventral, lateral, and dorsal views—T (trachea), S (syrinx), SR (syringeal ring), BR (bronchus). Drawings by RG Carveth. Adapted from Fig. III-5 in Degner (1988).

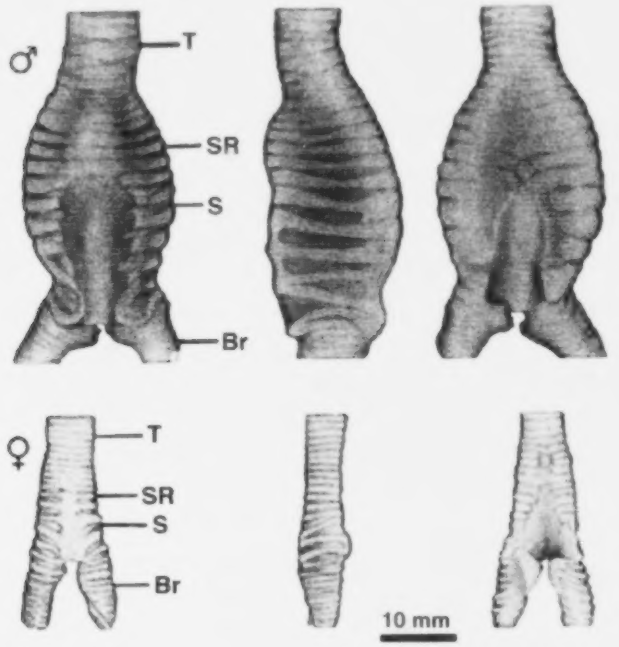
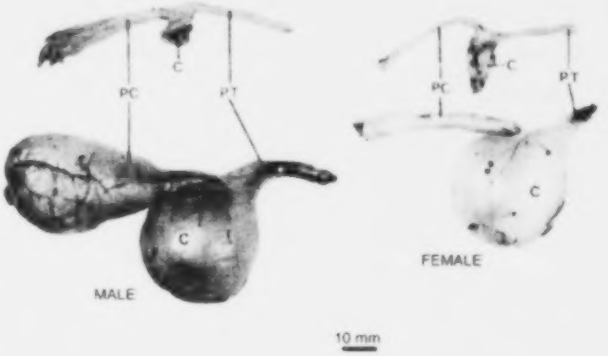


Fig. 9.9. Uninflated (above) and inflated *pars cervicalis* (PC), crop (C), and *pars thoracica* (PT) of males and females, lateral views. Adapted from Fig. III-7 in Degner (1988).



M. tracheolateralis and *M. sternotrachealis*, but that of the male is much the largest and most complex in terms of shape (Degner 1988). The *tracheolateralis* appears to pull the bronchi cephalad and inwards and to draw the trachea and syrinx cephalad. The *sternotrachealis* opposes the *tracheolateralis* and appears to draw the syrinx and trachea caudad, perhaps to steady the syrinx.

Male *D.o. fuliginosus* have, on average, more syringeal rings than females: means of 14.5 and 12.5, respectively (Degner 1988). Lengths of syringes of males and females averaged 36 mm and 14 mm; widths, 23 mm and 10 mm; and depths, 18 mm and 6 mm, respectively, with those of males significantly larger than in females in all cases. Internal tympanic membranes of males, the principal sound-producing membranes, are ~4–5 times thicker than in females. Thick membranes vibrate more slowly and may contribute to the generally low-frequency vocalizations of males (Degner 1983, 1988). According to Degner, none of these differences can be accounted for by differences in body size. Syringes of yearling males tended to be slightly smaller than in adult males, but not significantly so, but the sample of yearlings was small.

Fundamental frequencies of songs of coastal and interior males differ, with those of interior males lowest (Hjorth 1970; Degner 1988; and see 15.2.1(a)). Degner compared syringes of *D.o. pallidus* and *D.o. fuliginosus* as examples of interior and coastal subspecies, respectively. On average, *pallidus* had more syringeal rings, 16 versus 13. Lengths of syringes of *D.o. pallidus* and *fuliginosus* averaged 38 mm and 33 mm, and widths, 25 mm and 23 mm, respectively, significantly different in both cases. Syringeal depths averaged 18 mm in both races. The larger syringes of *D.o. pallidus* may explain, in large part, differences in fundamental frequencies of their songs (lowest in *pallidus*; see 15.2.1(a)), for the larger the syrinx, the lower the frequency of the song (Degner 1988).

Gross (1928), working with the heath hen (*Tympanuchus cupido cupido*), first proposed that the esophagus might be involved as an accessory organ in the production of song in some male grouse. Later, Honess and Allred (1942) and Clarke et al. (1942) showed that the anterior section of the esophagus of male sage-grouse, the *pars cervicalis*, is expandable. They postulated that the inflated esophagus causes swelling of the neck and apparent inflation of the lateral cervical apteria, the so-called "air sacs".

As in the prairie-chickens and sage-grouse, the esophagus of male blue grouse is expandable (Degner 1988). Degner found no difference in mean width of the uninflated *pars cervicalis* of adult males and females at its posterior end (7.2 and 6.8 mm, respectively), but that of males was over twice that of females at the anterior end (24.1 and 11.8 mm, respectively). Mean maximum width of the *pars cervicalis* of males was over four times that of females after experimental inflation (means of 68.0 mm and 15.9 mm, respectively, although inflatability of the crops did not differ (Fig. 9.9)). Differences between the sexes could not be accounted for by differences in body size. Degner concluded that only males have a *saccus esophageal*is (inflatable sac, the *pars cervicalis*) and postulated that when inflated it may serve as a resonating chamber to amplify sounds produced in the syrinx, as suggested for the heath hen (Gross 1928).

Extensibility of the esophagus of male sage-grouse is facilitated by the presence of large quantities of elastic fibres (Clarke et al. 1942). Esophagi of male blue grouse have not been examined histologically, but that is likely true for them. We think swelling of the neck region and exposure of the lateral cervical apteria of males during display is principally facilitated by inflation of the esophagus, coupled with flushing of the dermal layer of the apteria with blood and manipulation of the apteria and cervical feather tracts by superficial muscles of the neck.[18]

9.3 Synthesis

Blue grouse are seventh largest among world, and third largest among North American, tetraonines. They exhibit large sexual size dimorphism, exceeded among the tetraonines, only by the two capercaillie and two sage-grouse.

Body mass of adult and yearling males is relatively stable throughout the breeding season but that of yearling and adult females is very labile, peaking in early spring, and decreasing to an annual low at termination of incubation. Circumstantial evidence indicates yearling and adult males and females either maintain, or increase, body mass in winter. It varies among populations and appears more related to local situations than to subspecies.

Within populations, length of foot and wing parallel body mass. Among populations, however, foot parallels body mass but wing does not. Thus, foot varies among local populations, even within subspecies, while wing appears to be more closely related to subspecific designation. Coastal grouse have short wings and tails when compared to interior birds. These differences may be adaptations to the general types of habitats occupied by the two groups, more forested (coastal) and more open (interior).

On average, external measurements based mainly on bone, e.g., length of foot and tibiotarsus, show little, or no, difference between yearlings and adults, while those containing a large plumage component, e.g., wing and tail, show greater differences. Nevertheless, in virtually all external body measurements examined those of yearlings were >95% those of adults.

We found little seasonal change in size of the two major breast muscles or most internal organs of yearling and adult males from coastal British Columbia in spring and summer, consistent with data showing little seasonal change in body mass. An exception was that gizzard mass was greater in spring than summer, presumably a result of a shift in diet from conifer needles to less fibrous foods during this time. Breast muscles and most internal organs of yearling and adult females parallelled spring–summer changes in body mass.

Syringes of blue grouse are sexually dimorphic, with those of males much larger than in females. Those of interior males are larger than of coastal males and this correlates with low and higher frequency songs, respectively. Lower frequencies of interior males are likely a reflection of their larger syringes, likely the largest of any North American grouse. Males have an expandable esophagus that appears to be principally responsible for swelling of the neck during singing, contributes in part to exposure of the lateral cervical apteria during display, and may serve as a resonating chamber for sound produced in the syrinx.

Endnotes [Chapter 9]

1. Counting each of the two species of capercaillie, sage-grouse, and black grouse as one.

2. Masses in May are from females that may not have bred or from those in various stages of egg-laying and incubation. Since females lose mass during incubation, monthly means from this period are less than if all birds were examined just prior to, or during, laying.

3. Masses of broodless females in June are from birds incubating eggs, that may have lost nests (and had completed part of incubation), or that had not bred. Those of broodless females in July and August are mainly from non-breeders, or unsuccessful breeders but may include a few birds incubating eggs.

4. Differential migration might affect availability to hunters of certain classes of birds.

5. Bendell's (1955*b*) June–July data for females likely included some birds that had not completed incubation, and his hunter sample likely included some yearlings that had completed their primary moult and were identified as adults, lowering the mean for September. Either tends to obscure a post-incubation gain in mass.

6. Midsummer and late-summer masses can be affected by differential migration among age classes, for adult males leave territories beginning in June and some yearling males and non-breeding or unsuccessful yearling females begin their return to winter range in midsummer.

7. Most June masses of adult females at Sheep River (17/22) were from birds captured in the last 10 days of the month and represent mainly post-incubation birds.

8. Calculations are based on grand spring–summer means of 1273 g for adult males, 1112 g for yearling males, and means depicted in Fig. 9.1 for adult and yearling females.

9. By this time, females have begun to recover from seasonal lows, and this is likely when data from different populations are most comparable. A weakness is that some yearlings may be classified as adults, and the proportion may vary among populations.

10. Time of breeding may vary among populations, and in some samples brood and broodless females were separated, while in others they weren't.

11. Preliminary analyses suggest little difference in body size between birds at Comox Burn and Hardwicke Island, so necropsy data from these areas were combined. Data from banded birds were used for foot and wing measurements because of the large samples.

12. Breast muscles, heart (excess blood extruded), gizzard (with and without lining; contents removed), proventriculus, liver, spleen, and pancreas were weighed, and the small intestine, colon, and one cecum were measured linearly. Mass of the gizzard with lining is used for seasonal comparisons of this organ.

13. If months were contiguous and means did not differ, data were combined to produce a mean for the longer period. If there were no monthly differences, a grand spring–summer mean was computed.

14. Pendergast and Boag (1973, p. 312) found larger gizzards in spruce grouse in winter than summer. They thought large gizzards in winter were related to increased mass associated with a "response to the tougher foods".

15. Samples of *D. o. fuliginosus* were from early stages of forest succession, where most males sing from the ground.

16. Those weighing less, or the same, on post-initial captures may be partly explained by amount of fill in the crops. No negative mass change exceeded 50 g, while increases ranged up to 270 g.

17. Greenewalt (1968) indicated that the song of spruce grouse is of lower frequency than in blue grouse, but Greg Budney (letter, 26 February 1993) says the "spruce grouse" recording on which his conclusion was based is from a blue grouse, with which we concur.

18. True air sacs also might play a small role but this has not been examined in any grouse.

CHAPTER 10

Reproduction

> *The biological problem of the perpetuation of the species has been solved in a bewildering variety of ways in nature.*
>
> AV Nalbanov (1976)

Reproduction, in the evolutionary sense, represents the culmination of life's efforts and is not completed until one's offspring begin to reproduce. More proximately, it spans the period each year from the beginning of reproduction until one's young are independent. Here, we examine reproductive events and parameters from time of breeding to birth of young. We include nests, an external but important component of the reproductive cycle in birds. Post-hatch biology of chicks and behaviour of breeding birds are considered in Chaps. 11 and 15, respectively.

10.1 Breeding age

10.1.1 First breeding

(a) *Males*. Male blue grouse are considered promiscuous (Bendell and Elliott 1967; Hjorth 1970; Wiley 1974; De Vos 1979). Yearlings (~1 year old) usually do not breed (Bendell and Elliott 1967), although many yearling females do, a condition referred to as *sexual bimaturism* (Wiley 1974). Controversy exists as to whether yearling males "delay" (Wiley 1974; Jamieson 1985; Lewis and Jamieson 1987), or are prevented from, breeding through competition with adults (Wittenberger 1978). Physiologically, at least some can breed (Standing 1960; Hannon et al. 1979) and may replace males removed from breeding territories (Bendell et al. 1972; Zwickel 1972*a*, 1980), offering support for Wittenberger's view. Some yearlings, however, do not settle on vacant territories even though residents have been removed (Lewis and Zwickel 1980), consistent with the delayed breeding hypothesis (Lewis and Jamieson 1987).

(b) *Females*. We once thought that virtually all yearling females that come onto breeding range on Vancouver Island attempt to breed (Zwickel and Bendell 1967*b*). Circumstantial evidence from reproductive tracts (Standing 1960; Hannon and Zwickel 1979) and removal studies (Bendell et al. 1972; Zwickel 1972*a*, 1980) now indicate some do not, consistent with an earlier report by Bendell (1955*a*). In 1985 and 1986, we equipped 23 females with radios in Nevada, California, Montana, and British Columbia. All adult, but only 3 of 10 yearlings are known to have nested. Other evidence from birds equipped with radios supports this view (Sopuck 1979; Hines 1986*a*). Boag (1964) reported that many yearlings in a population in Alberta remained in flocks throughout spring and summer and that only 14% bred. Three brood hens examined for age by King (1971) in subalpine Vancouver Island were adults, and three yearlings examined for ovarian activity were negative. Clearly, some yearling females do not breed in at least some years and populations. There is no clear evidence for non-breeding adults.

Two principal explanations have been advanced for non-breeding among yearling females. Boag (1964) suggested many in the Sheep River area were physiologically immature, a result of late hatches and insufficient time to mature before onset of winter. The second, and more controversial explanation, is that intrasexual social interactions may exclude some females from breeding. Studies in which females were removed from breeding range and replaced by yearlings are consistent with this view (Bendell et al. 1972; Zwickel 1972*a*, 1980). Intrasexual aggression among females that could cause exclusion exists (Hannon 1980; Lewis 1984*a*; Bergerud and Butler 1985). Both explanations may apply, and their impact may vary among years and populations.

10.1.2 Longevity and breeding

Once reproductively active, blue grouse apparently attempt to breed throughout life, as suggested for older known-aged birds at Comox Burn (Table 10.1). For example, 18 older males sang (evidence of territoriality), or were on territories they held in other years, in 92% of 132 adult years monitored. All were singing ($n = 17$), or on territory, when last seen, presumably the last year alive. Among 12 older females, they were found with brood in 78% of 64 yearling and adult years monitored. Of these birds, 10 were with brood in the last year seen, presumably the last year alive and approximately the same proportion as for all banded adults for which reproductive status was known. Although samples are small, once breeding, most males and females in our data indicate that they do so throughout life.

10.2 Time of breeding

Time of breeding in blue grouse is seasonal, as in most north-temperate species. Its onset may vary among years, age classes, local populations (Zwickel 1977), or broad geographic regions (Bendell and Zwickel 1984).

Table 10.1. Territorial occupancy of oldest banded males[a] and breeding status of oldest banded females at Comox Burn, 1962–1978.

	Number	Percent
Males ≥9 years of age (mean ≥9.7 years)	18	
Years seen[b]	132	82
Years known alive but not seen	28	18
Years seen, singing	121	92
Years seen, not singing	11	8
Singing in last year seen[c]	17	94
Females ≥7 years of age (mean ≥7.8 years)	12	
Years seen[b]	64	74
Years known alive but not seen	23	26
Years seen, with brood	50	78
Years seen, without brood	14	22
With brood in last year seen	10	83

[a] Singing and location considered as evidence of territoriality.

[b] Identified by bands in a given year.

[c] One bird was not seen singing but was on territory used in other years.

10.2.1 Timing of breeding events

Breeding, in a broad sense, involves a number of related events, including copulation, laying of eggs, incubation, and hatching and raising of young. Time of hatch is most easily determined, and from it, one can extrapolate backwards to estimate timing of the other parameters.[1]

We illustrate timing of breeding parameters with data from 5 years at Comox Burn when peak hatch occurred in the same 2-week period, neither early nor late (Fig. 10.1). There is a strong skew to the right of all events. This "tail" reflects, largely, second breeding attempts following loss of a first nest. The four events shown each span a period of ~10 weeks and, all combined, ~15 weeks. Addition of the earliest date documented for copulation, 22 April, and latest date of hatch, 12 August, increases the range to ~16 weeks. The pattern at Hardwicke Island was essentially the same as at Comox Burn except ~2 weeks shorter in most years, a reflection of higher nesting success (10.6.5(a)) and less renesting than at Comox Burn.

Distribution of dates of hatch in other areas may differ. The longest run of data, 6 years, comes from *D.o. obscurus* from Colorado (Hoffman 1981). We combined Hoffman's annual samples by bringing peaks of hatch into synchrony with one another and compared the pattern there to that at Comox Burn (Fig. 10.2). There is no strong skew in the Colorado data, with peak hatch more centrally located than at Comox Burn, a significant difference between areas [1]. Samples from four other interior populations have patterns similar to that from Colorado: *D.o. richardsonii*, Alberta (Boag 1966); *D.o. obscurus*, Utah (Weber 1975); *D.o. obscurus*, Wyoming (Harju 1974); and *D.o. pallidus*, Montana (Mussehl and Schladweiler 1967). There may be little renesting in these populations, where breeding is relatively late (Fig. 10.3). A single annual sample (1968) from a *D.o. pallidus* population in the Methow Valley (FC Zwickel, unpublished) is skewed to the right, as for *D.o. fuliginosus* on Vancouver and Hardwicke islands. Breeding there is very early (Fig. 10.3), allowing more time for renesting.

10.2.2 Variation in time of breeding

(a) *Variation within and among local populations*. Within a given area, breeding may vary among years (Zwickel 1977). In "early" years peak hatch at Comox Burn began ~1 week

Fig. 10.1. Timing of copulation, first eggs laid, initiation of incubation, and hatch for banded females at Comox Burn$_{cp}$, 1969, 1970, 1974–1976. Data combined.

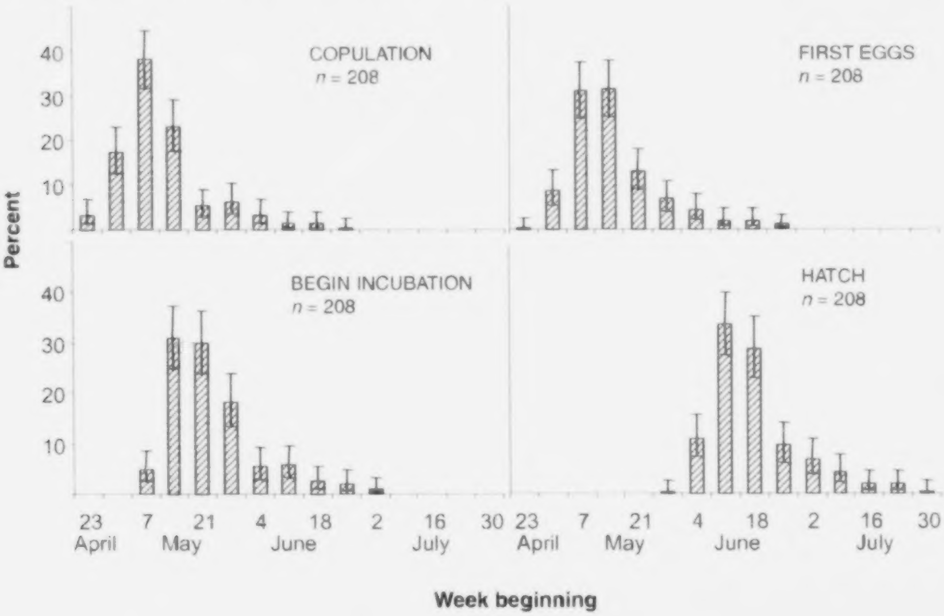


Fig. 10.2. Chicks hatching per week (%), Colorado and Comox Burn. Colorado data are from analyses of hunting samples, courtesy of RW Hoffman.

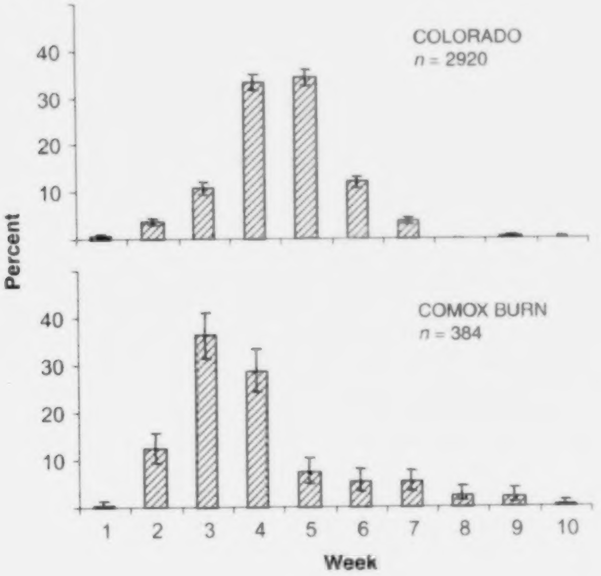


Fig. 10.3. Geographic variation in time of peak hatch, increasing latitude from bottom to top. Latitude at Duck Creek, 39°17′; Centennial, 41°18′; Brownlee, 44°23′; Comox Burn, 49°42′; Hudson Bay Mt., 54°45′. If data are available for more than 2 years, the peak is represented by the median, or modal, 2-week period among years.

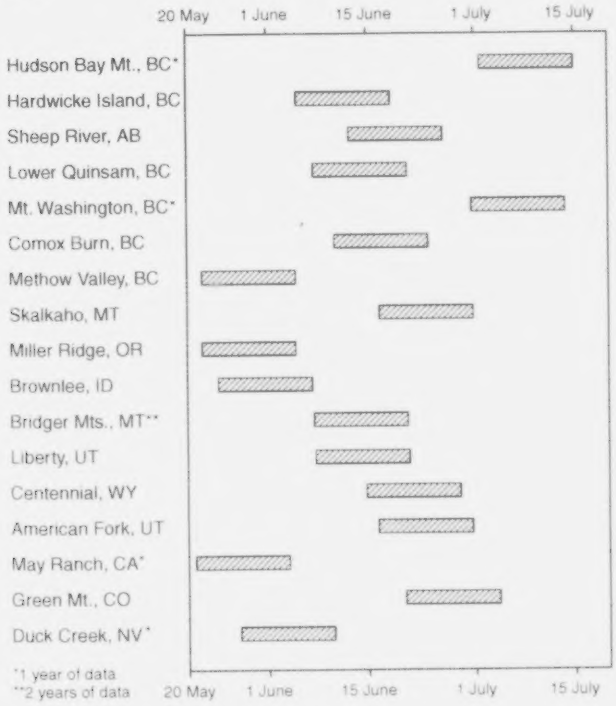
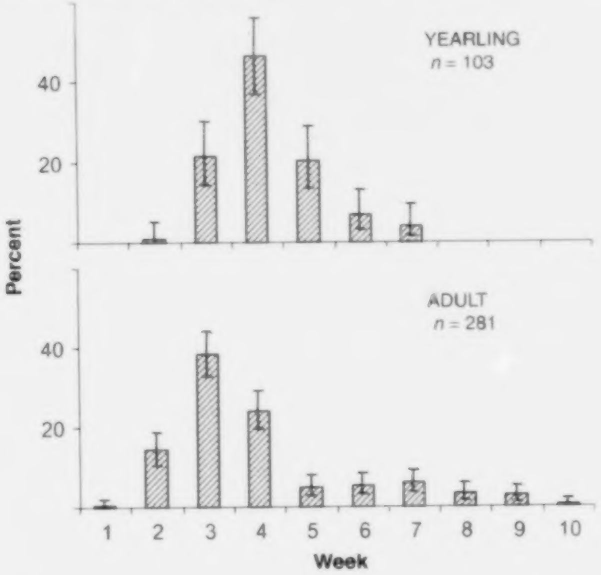


Fig. 10.4. Nests hatching per week (%) for yearling and adult females, Comox Burn, 1969–1978.



earlier than in "normal" years, and in "late" years, ~1 week later than in normal years. Thus, although the peak was usually ~2 weeks in length, its location in a given year varied within a range of 4 weeks. Similar data are available for Hardwicke Island and some interior populations (Mussehl and Schladweiler 1967; Harju 1974; Weber 1975; Hoffman 1981), although the outside range for an area may be up to 5 weeks. Variations among years on the same area are likely related to weather, either alone, or indirectly through interactions with vegetation (Zwickel 1977). Variations among nearby local areas may relate to climate. For example, although Comox Burn and Tsolum Main are only 2–3 km apart, breeding at Tsolum Main was consistently ~1 week later than at Comox Burn and this is correlated with differences in altitude, temperature, precipitation, and the disappearance of snow at the two areas (Zwickel 1977). Breeding in nearby subalpine habitat was ~1 month behind that at Comox Burn (King 1971).

(b) *Geographic variation.* Geographic variation can be marked (Fig. 10.3[2]). In studies with only 1 or 2 years of data, we do not know whether these were early, normal, or late years for those areas, and the normal peak might be ±1 week of that shown. There is no clear relationship between time of hatch and latitude. Clearly, photoperiod (as reflected by latitude), although almost certainly involved in bringing birds into breeding condition, is not "fine-tuning" time of breeding. Local climate and weather and (or) their interactions with vegetation are likely most important in that respect.

(c) *Yearling and adult females.* Time of breeding differs in yearlings and adults. Yearlings lagged behind adults by ~1 week (Zwickel 1977) in virtually all years ($n = 19$) at Comox Burn (Fig. 10.4) and Hardwicke Island. Earliest and latest recorded hatch dates for adults at Comox Burn were 30 May and 12 August, and for yearlings, 9 June and 22 July, respectively. Data from Ash River indicate an average difference between age classes of ~6 days, with yearlings latest (Redfield

1975). Three reasons may explain later breeding by yearlings: (1) late arrival on breeding range, (2) relative immaturity, likely not exclusive from (1), and (3) inhibition by adults (Hannon et al. 1982). Hannon et al. suggested that many yearlings cannot localize for nesting until most adults are incubating eggs, and is controversial (Bergerud and Butler 1985). All three explanations may contribute to differences between the age classes.

10.3 The gonad cycle

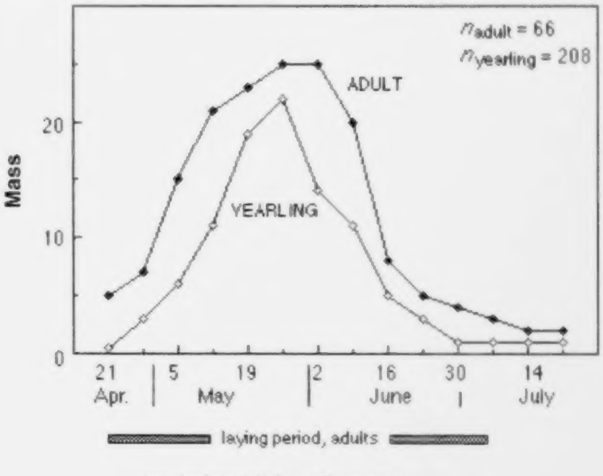
Breeding season begins with movements onto spring and summer range. Whether short or far (migratory), these movements are almost certainly hormonally controlled and at least partly photoperiodically induced. Breeding season thus begins on winter range.

Two studies of gonadal cycles of blue grouse involve one interior race, *D.o. pallidus* (Standing 1960), and one coastal race, *D.o. fuliginosus* (Hannon et al. 1979). We use the latter study to describe male and female gonadal cycles because of its larger samples.

10.3.1 Females

Hannon et al. (1979) presented data on diameters of largest ovarian follicles and weights of oviducts for birds collected at Comox Burn. Both sets of data followed the same general pattern, and we illustrate those for oviducts (Fig. 10.5). Earliest oviducts of adults that were examined suggested they began to recrudesce before arrival on breeding range, i.e., oviducts in late April, soon after arrival, were heavier than in late July, after regression in the previous breeding season. Oviducts of yearlings were small in early spring, suggesting that most development occurs after arrival on breeding range. Oviducal development is rapid, with that of yearlings ~7–10 days behind that of adults. Oviducal regression began ~7–10 days earlier than in adults. A skew to the right of oviducal mass of adults likely reflects renesting. Clearly, adults began laying eggs earlier and had a more extended laying period than yearlings. As well, their oviducts peaked at a higher mean mass than in the younger birds. Nevertheless, the largest ovarian follicles were equivalent in the two age classes (Hannon et al. 1979). Ovaries collected from yearlings killed by hunters in late August were significantly lighter than those of adults, so even then gonads of yearlings were less developed, or more regressed, than in adults.

Fig. 10.5. Mean weekly oviduct mass (g) of yearling and adult females, eastcentral Vancouver Island. Data extrapolated from Fig. 2 of Hannon et al. (1979).



Standing (1960) did not separate his data on the reproductive cycle of female *D.o. pallidus* by age class, but the general picture was virtually identical to that of *fuliginosus* except that all events occurred earlier.

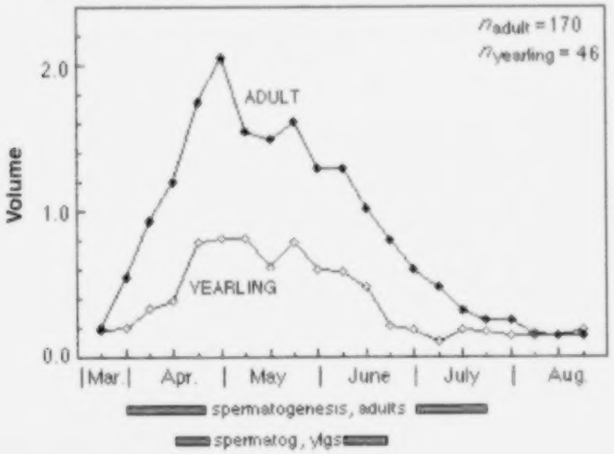
(a) *Plasma calcium, as an index to reproductive status.* Hannon (1979) developed a technique to identify laying females without having to sacrifice them. She found a high positive correlation between plasma calcium and mass of the oviduct and development of ovarian follicles. Ovarian follicles <6 mm in diameter grew slowly, "slow recrudescence", but at ~6 mm, growth increased markedly, "rapid recrudescence", taking 9–10 days to reach ovulation size. Plasma calcium levels ≤160 ppm identified females in "slow" recrudescence, levels >160 ppm, identified laying females, those in "rapid" recrudescence. Maximum calcium levels were attained at 1–4 days prior to ovulation and declined slightly during laying, presumably reflecting calcium withdrawal for incorporation into eggshells. Post-laying females were identified as those with a brood patch.

More than 90% accuracy was attained in using these criteria to classify 95 females whose reproductive status was known from examination of ovaries and oviducts. Plasma calcium of 31 in slow recrudescence averaged 118 ppm (range = 70–160 ppm), that of 64 in rapid recrudescence averaged 260 ppm (75–470 ppm; all but 3 exceeded 160 ppm), and that of 41 post-laying females, 110 ppm (55–200 ppm). Maximum calcium level in 37 males was 160 ppm.

10.3.2 Males

The earliest samples of testes of *D.o. fuliginosus* were collected after birds had come onto breeding range, and, although sample sizes were small, suggest recrudescence had begun (Fig. 10.6), i.e., testis volumes in late March were larger than in late summer, following regression. The pattern of recrudescence and regression in yearlings and adults is similar, but different in detail. Testes of adults recrudesce rapidly, but those of yearlings pass through a slow phase. Both age classes peak at about the same time, but yearlings at a lower volume; ~45% that of adults, even though yearling body mass is ~90% that of adults. Yearlings pass through all stages of spermatogenesis, and their active breeding condition lasts ~9 weeks, that of adults ~15 weeks. Sperm of yearling and adult aviary birds are equally viable, and one aviary yearling bred with a female that produced fertile eggs (Hannon et al. 1979). Although full regression of yearling testes occurs ~4 weeks earlier than in adults, active breeding condition in both age classes exceeds (adults) or approximately equals (yearlings) the entire period of copulation in females (Fig. 10.1), even for second nests. Testis volumes of males from subalpine areas adjacent to Comox Burn indicated that the gonadal cycle was essentially

Fig. 10.6. Mean weekly testis volumes (cc) of yearling and adult males from eastcentral Vancouver Island. Data extrapolated from Fig. 3 of Hannon et al. (1979).



the same as described above, but retarded by ~1 month (King 1971).

The testis cycle of *D.o. pallidus* from the Methow Valley (Standing 1960) was virtually identical to that shown in Fig. 10.6 except that all events occurred ~10–15 days earlier. Yearling males there also passed through all stages of spermatogenesis. These data indicate yearling and adult males produce viable sperm, even though yearling testes do not attain the size of those of adults.

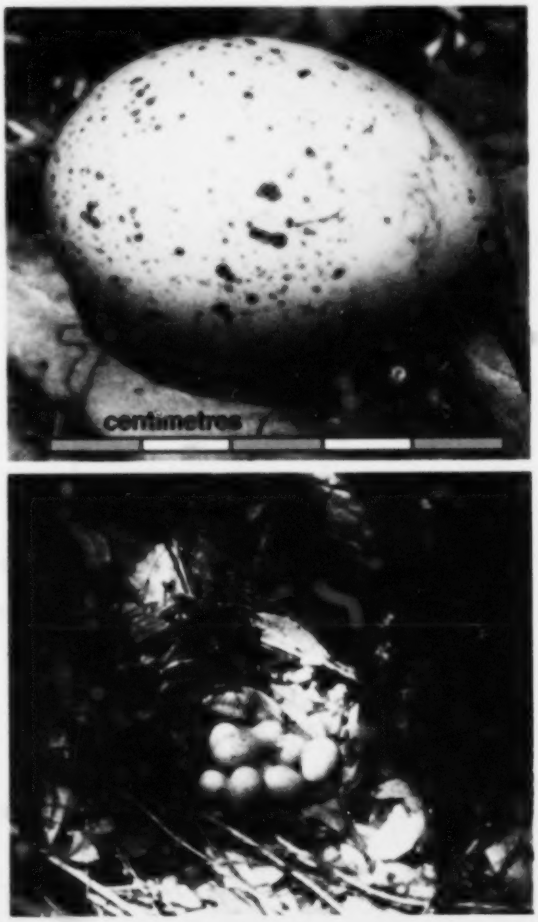
10.4 Eggs

Fertilized avian eggs are the first free-living stage of new individuals. Although physically free from parents, once laid, they are still dependent on the female (in most birds), their own composition, and environmental conditions.

10.4.1 Shape and colour

Eggs of blue grouse most closely approach *short subelliptical* (Palmer 1962) in shape (Fig. 10.7), with those in the occasional clutch more *subelliptical*. Background colour of freshly laid eggs usually varies between *pale pinkish buff* (121D, Smithe 1975) and *beige* (219d). They are normally more or less speckled, or lightly splotched, with darker browns that may vary among *russet* (34), *Prout's brown* (121a), *burnt sienna* (132), or *warm sepia* (221a). Those in the occasional clutch may be unmarked. Speckles are usually ≤1 mm across and splotches up to 3.5 mm across. Shapes and colours are usually consistent within, but may vary among, clutches. Rarely, two distinctive shapes or colours may be found in the same nest, an indication that two hens may have laid eggs in that nest. Colours fade rapidly when exposed to strong light, likely varying over the course of laying and incubation, and among sites with differing exposures to light.

Fig. 10.7. *D.o. fuliginosus* egg and its nest in old-growth forest, May Ranch. Shape, colour, and speckling are typical of freshly laid eggs. Photos by MA Degner.



10.4.2 Size

Eggs lose water during incubation, making it difficult to compare masses among clutches found at different stages of incubation. Volume and fresh mass, that prior to incubation, can be estimated with reasonable accuracy, however, from measurements of length and breadth (Hoyt 1979). We used Hoyt's methods to estimate volumes and fresh masses for eggs from our studies and for others reported in the literature.[3]

(a) *Eggs of yearling and adult females.* Mean lengths, breadths, volumes, and fresh masses of eggs of yearlings from Vancouver and Hardwicke islands[4] (Table 10.2) were significantly less than those of adults [2a–d]. Volumes and masses were each less by 7% in yearlings than adults (2.6 mL and 2.7 g less, respectively). Mean masses when found, yearlings, 31.8 ± 0.40 g (n = 81), and adults, 34.6 ± 0.33 g (n = 151), were 9% and 8% less than calculated fresh masses for each age class, respectively. The latter figures presumably represent percent water loss between eggs when laid and those weighed at various stages of incubation.

Table 10.2. Mean lengths, breadths, volumes,[a] and fresh masses[a] of eggs of yearling and adult females, Vancouver and Hardwicke islands, data combined.[b]

	Yearling	Adult
Length (cm ± SE)	5.2±0.02	5.3±0.02
Breadth (cm ± SE)	3.6±0.01	3.7±0.01
Volume (mL ± SE)	33.7±0.33	36.3±0.30
Mass (g ± SE)	34.9±0.35	37.6±0.31

[a] Calculated from length and breadth measurements as per Hoyt (1979).
[b] Number of clutches/eggs: yearling, 32/88; adult, 45/144.

Table 10.3. Fresh egg masses[a] (g, mean ± SE) of adult females among areas.

Area	No. of clutches	No. of eggs	Mass
British Columbia[b]	45	144	37.6±0.31
May Ranch	2	16	29.6±0.41
Duck Creek	2	15	32.6±0.41
Skalkaho	4	26	28.8±0.39

[a] Fresh mass is that prior to start of incubation. Calculated from length and breadth measurements as per Hoyt (1979).
[b] Data from Vancouver and Hardwicke islands combined.

(b) *Loss of mass during incubation.* Rahn and Ar (1974) reported that the typical egg loses 18% of its initial weight during incubation. Hoyt (1979) suggested 16%. We have initial masses and those taken 2 days before hatch for four fresh eggs incubated in our aviary, three from one clutch. These eggs lost a mean of 14% (13.4%–14.9%) of their initial masses. Total losses were likely greater because eggs begin to lose water immediately after being laid (Hoyt 1979) and because final masses were taken prior to hatch.[5] We also have data on mass of eggs under incubation when found, and 2 days before they hatched (11 clutches, 35 eggs). They lost, on average, 0.24 g/day, a total of 6.24 g extrapolated over a 26-day incubation period. This is 17.2% of mean fresh egg mass, 36.2 g at Comox Burn. In blue grouse, loss likely equals, or exceeds, the 16% predicted by Hoyt.

(c) *Variations in mass within and among clutches.* We examined these parameters with clutches of 16 yearlings and 26 adults from Vancouver and Hardwicke islands. Mean fresh masses of all eggs of yearlings and adults were 34.7 ± 0.47 g and 37.8 ± 0.33 g, with coefficients of variation (CVs) of 11.47 and 9.77, respectively. Within clutch CVs were 4.26 and 5.27, and among clutch CVs, 6.12 and 9.29, respectively. There was greater variation among than within clutches in both age classes, suggesting a stronger inherent component in the determination of egg size within than among age classes of females. This is consistent with observations that colour and shape differ less within than among clutches. Variation among clutches might reflect either intrinsic (e.g., genetic) or extrinsic (e.g., nutritional) influences, or both.

(d) *Variations in mass among populations.* Our samples of egg masses from other than Vancouver and Hardwicke islands are small, especially with respect to numbers of clutches. Nevertheless, they suggest interpopulation differences. Mass of those of adult females from coastal British Columbia were significantly heavier than from the May Ranch, Duck Creek, and Skalkaho (Table 10.3) [3a–c]. Those from Duck Creek were larger than from the May Ranch and Skalkaho [4], but the latter two did not differ [5]. Thus, within these samples, *D.o. fuliginosus* from coastal British Columbia had large eggs; *D.o. oreinus* from Duck Creek, intermediate-sized eggs; and *D.o. fuliginosus* from northern California and *D.o. pallidus* from western Montana, small eggs. High environmental temperature tends to reduce egg size (Warren 1949),[6] and our data fit that pattern, i.e., larger in coastal British Columbia and smaller in the warmer interior and more southern coastal population at the May Ranch. If these data are representative, egg size correlates more with local populations than with subspecies, body size of breeding birds (see Tables 9.1 and 10.3), or coastal versus interior habitats. This generalization needs testing with larger samples from more areas.

Lengths and breadths of eggs are occasionally reported in the literature, but ages of hens, areas from which samples came, and, usually, numbers of clutches, are unknown. We calculated fresh masses from these reports for six subspecies (Table 10.4). All suggest smaller eggs, some much smaller, than adult *D.o. fuliginosus* from our studies in British Columbia. Note especially, that Bent's largest sample, 92 eggs of *D.o. fuliginosus*, likely a composite sample from several areas, suggests a mass that is >3 g less than eggs from yearlings (Table 10.2) in our sample. Size varies among local populations, even within subspecies.

(e) *Dwarf eggs.* We found two dwarf eggs at Hardwicke Island. The smallest, 7.2 g, was in a clutch of four (Fig. 10.8), among which one weighed 31 g and the other two each weighed 34 g (weighed on day of hatch), a mean of 33 g for the latter three. The dwarf egg weighed only 22% the mean of the other eggs, all of which hatched. The small egg did not hatch and had no yolk. Domestic chicken eggs less than 20% of normal mass do not have yolks (Romanoff and Romanoff 1949).

The second dwarf egg weighed 22 g, with three others in this clutch weighing 33 g, and one, 35 g, a mean of 33.5 g (weighed on about day 15 of incubation). The small egg was 66% the mean mass of the others and disappeared prior to hatch; all others hatched. Both females that produced dwarf eggs were yearlings.

(f) *Mass of newly hatched chicks as a percent of egg mass.* Mean mass of newly hatched chicks at Comox Burn, 25.8 g, is ~70% of fresh egg mass there and ~84% of egg mass at time of hatch. That of new chicks at Skalkaho, 19.4 g, is ~67% of fresh egg mass there and ~80% of egg mass at time of hatch.

10.4.3 Thickness of eggshells

We measured shell thicknesses of hatched eggs from Comox Burn ($n = 76$ eggs, 21 clutches), Hardwicke Island (28 eggs, 10 clutches), the May Ranch (7 eggs, 1 clutch), the Methow Valley (7 eggs, two clutches), and Skalkaho (10 eggs, two clutches).[8] With one exception, Hardwicke, shell thickness did not differ among areas [6a, b]. Mean thickness at Hardwicke Island, 0.23 ± 0.004 mm, was significantly less than that of 0.24 ± 0.001 mm for all other areas combined [7]. Samples from areas other than Comox Burn and Hardwicke

Table 10.4. Fresh egg masses[a] (g) of blue grouse among subspecies, as reported by others.

Subspecies	n_{eggs}	Mass	Source[b]
D.o. obscurus	54	32.0	1
D.o. richardsonii	32	28.1	1
D.o. howardi	5	35.2	1
D.o. sierrae	23	31.9	1
D.o. sierrae	12	34.3	2
D.o. fuliginosus	92	31.4	1
D.o. sitkensis	4	34.0	1
The species in general[c]	?	31.4	3

[a] Masses calculated from length and breadth measurements presented by authors; calculations by us as per Hoyt (1979).

[b] 1, Bent (1932); 2, Grinnell et al. (1918); 3, Johnsgard (1983).

[c] The source of Johngard's measurements is unclear. He used a K_w of 0.552, as suggested by Stonehouse (1966) for birds in general, to calculate a mass of 33 g. We used a K_w of 0.528, as calculated by us for blue grouse in general.

Island are small, but if representative of areas from which they came, suggest the ratio of shell thickness to egg size might vary among areas, e.g., eggs were largest at Comox Burn and Hardwicke Island but smaller at the other areas. These data also indicate this ratio is greater at Comox Burn than at Hardwicke Island, local populations ~140 km apart.

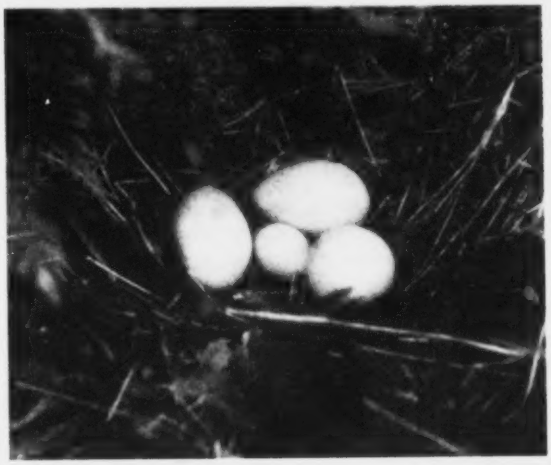
10.4.4 Rate of egg-laying

Caswell (1954*b*) reported a laying rate of 1 egg per 1.75 days for the last 4 eggs in an 8-egg clutch of *D.o. pallidus* in Idaho, and Standing (1960), a laying rate of 1 per 1.5 days for the last 5 eggs of a 9-egg clutch of *D.o. pallidus* in Washington State. Caswell checked his nest only periodically, but Standing did so each day. We have partial data from each of five nests at Comox Burn and Hardwicke Island that suggest a slightly longer laying interval. These nests were checked periodically, and with data from all combined, 16 eggs were layed in 32 days, a mean interval of 2 days/egg. The shortest interval between any 2 eggs was 1 day, and the longest, 3 days.[9] Two days may be the best estimate of the laying interval for grouse on our study areas, but even these data are equivocal because of the small samples. The estimate by Standing (1960) of 1.5 days/egg is generally consistent with rates reported for most other grouse (Johnsgard 1983).[10]

10.4.5 Eggs outside nests (drop eggs)

Rarely, a single egg is found in the field. Such incidents have been poorly documented, but we estimate they would number <10 during all years of study. These might represent either drop eggs (eggs laid at random (Buss et al. 1951)) or eggs displaced from nests that were not found—eggs are occasionally rolled out of a nest when the female is flushed. At least once at Comox Burn, a soft-shelled (uncalcified) egg was found, almost certainly a drop egg. Drop eggs are rare, consistent with the close correspondence between numbers of postovulatory follicles and size of clutches (Hannon 1981).

Fig. 10.8. Dwarf egg in nest at Hardwicke Island.



10.4.6 Eggs as a percent of female body mass

Mean mass of individual eggs of yearlings (Table 10.2) is 3.8%, and that of adults, 3.7%, of mean May body masses (Fig. 9.1) in each age class. An average yearling clutch at Comox Burn (5.5 eggs, 192.1 g) weighs 20.7%, and that of adults (7.0 eggs, 263.8 g), 25.9%, of mean May body mass in each age class.[11] Johnsgard (1983) calculated individual egg mass of blue grouse as 3.6%, and total clutch mass as 22.4%, of female body mass. He did not separate data for yearlings and adults, but his values are essentially the same as ours. Variations in egg and clutch sizes among populations will alter these calculations slightly. For example, with similar egg and body sizes, but smaller clutches than at Comox Burn (Zwickel et al. 1988), yearling and adult female clutches at Hardwicke Island represent 19.0% and 21.7% of May body masses. The percent individual egg mass to female body mass of blue grouse ranks ninth, and percent clutch mass to female body mass, fourteenth, among 16 species of grouse considered by Johnsgard (1983). The relatively low ranking of blue grouse reflects its relatively large body and small clutch size.

Calculations of clutch mass above are based on first nests, but many blue grouse may renest (Sopuck and Zwickel 1983). Should a yearling renest (mean clutch = 4.5 eggs at Comox Burn), the total mass of eggs (349.1 g) produced in a year would represent 37.6% of her mean May body mass. A renesting adult (mean clutch = 5.7 eggs) would produce 476.9 g of eggs, 46.8% of her mean May body mass. With age classes combined, a mean of 42.2% for blue grouse approximates the first clutch–body mass relationships of female hazel grouse (*Bonasa bonasia*), 42.7%, and ruffed grouse, 43.7% (Johnsgard 1983), species in which females are relatively small but that produce large clutches.

10.5 Nests

Nests are a principal component of the environment in which eggs are laid, incubated, and hatched. Their placement and construction contribute to the environmental regimen of the eggs and hen during incubation, to protection of the incubating parent and eggs from predation, and to the ability of the parent to complete incubation. A successfully reproducing female spends ~7% of her annual cycle on the nest (see 15.3.2(b)).

10.5.1 Sites

Nest sites appear to be chosen by the female. They are virtually always on the ground, and well away from nests of conspecifics. They are most often outside territories of males, perhaps to avoid repeated courtship advances. There may thus be both physical and social constraints that influence sites selected for nests.

(a) *Site characteristics*. Over the range of blue grouse, nest sites vary (Fig. 10.9; see also Figs. 7.11, 10.7, 10.8, 10.10). They are found on recent burns with virtually no plant cover (Redfield et al. 1970; Zwickel and Bendell 1972*a*) and in virtually all community types occupied in breeding season, from sea level to subalpine. Among 620 nests from throughout the range of blue grouse, all but two were on the ground (two coastal nests were on low stumps). Among 612, >98% had some overhead cover. This cover may be as little as a single dead twig or complete cover by logs, stumps, or overhanging rocks or vegetation. In early coast forest seres on Vancouver and Hardwicke islands, 90% were under small conifers or logs, stumps, snags, or logging slash (Table 10.5). Broad-

Fig. 10.9. Variation in nest sites: all are *D.o. pallidus* in northcentral Washington on the left; all are *D.o. fuliginosus* on Vancouver Island on the right. Females in upper photos are incubating; note the more pale and grayish hue of the *pallidus* female than in the *fuliginosus* female. See also Figs. 7.11, 10.7, 10.8, and 10.10.

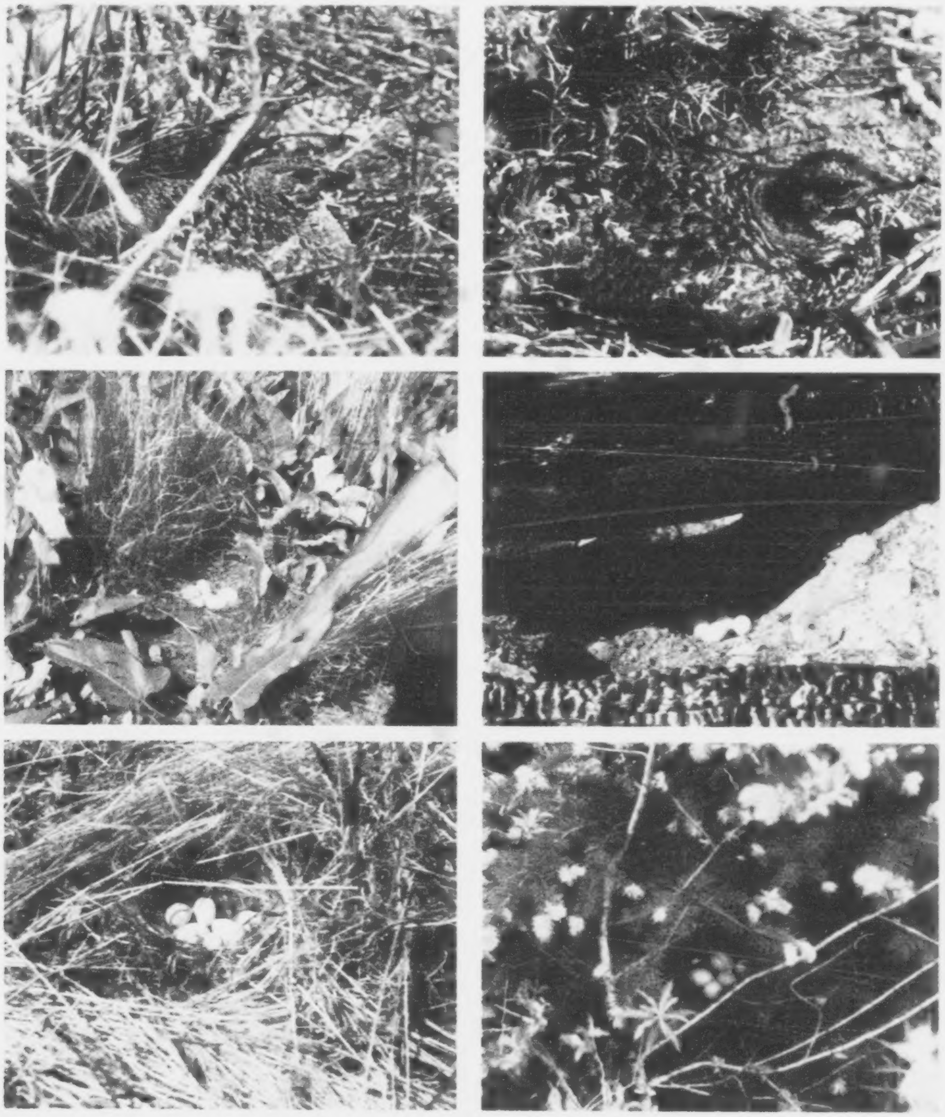


Table 10.5. Kinds of overhead cover at nests (%) in early coast forest seres[a] at Comox Burn and Hardwicke Island.

Kinds of cover	Comox Burn	Hardwicke Island	Total
Broad-leaved herb	1	1	1
Shrub	8	5	7
Small deciduous tree	4	0	2
Small conifer	61	61	61[b]
Log, stump, snag, or slash	27	32	29[c]
Rock	0	1	<1
No overhead cover	<1	1	1
n	317	170	487

[a] ≤ 20 years post-logging or fire.

[b] 75% of those under conifers on Vancouver Island were under Douglas-fir, 12% under western hemlock; 18% at Hardwicke Island were under Douglas-fir, 70% under western hemlock. This reflects a different availability of the two species at the two areas.

[c] 84% were under logs.

Table 10.6. (*a*) Kinds of overhead cover at nests (%) in relation to stage of vegetation in early coast forest seres (≤20 years post-logging or fire). (*b*) Differences in overhead cover at nests at Comox Burn$_{cp}$, 1962–1978.[a]

	Stage of vegetation[b]			
(*a*) Early seres	Very open	Open	Dense	Very dense
Broad-leaved herb	2	<1	0	0
Shrub	7	6	6	0
Small deciduous tree	5	1	0	0
Small conifer	38	71	78	100
Log, stump, snag, slash	47	21	17	0
Rock	0	<1	0	0
No overhead cover	1	0	0	0
n	150	262	36	2

(*b*) Comox Burn	1962–1965	1969–1973	1974–1978
Broad-leaved herb	0	0	2
Shrub	0	5	4
Small deciduous tree	9	5	0
Small conifer	21	74	84
Log, stump, snag, slash	70	16	11
n	33	58	55

[a] 1962–1965 (1–4 years post-wildfire), 1969–1973 (8–12 years post-wildfire), and 1974–1978 (13–17 years post-wildfire).

[b] As per Bendell and Elliott (1967).

Table 10.7. Kinds of overhead cover (%) at nests in young coast forest, interior forest, and interior shrub-steppe habitats.

Overhead cover	Young coast forest[a]	Interior forest[b]	Interior shrub-steppe[c]
Broad-leaved herb	1	2	8
Grass	0	7	18
Shrub	7	43	70
Small deciduous tree	2	0	0
Small conifer	61	13	0
Large conifer	0	2	0
Log, stump, snag, slash[d]	29	13	2
Overhanging rock	<1	20[e]	0
No overhead cover	1	2	2
n	487	61	61

[a] Vancouver and Hardwicke islands, seres ≤20 years post-logging or fire.

[b] Composite sample from Montana, Colorado, Idaho, Alberta. Interior forests are often open and occur as a mosaic with shrub-steppe communities. Sources: Boag (1958, pers. comm.), Heebner (1956), Hoffman (1981), Mussehl (1963*b*, *c*), FC Zwickel.

[c] Composite sample from Idaho, Montana, Nevada, Utah, Washington. Sources: Caswell (1954*b*), Heebner (1956), Mussehl (1960), Schotellius (1951*a*), Weber (1975), FC Zwickel.

[d] In coast forest 84% were under logs; in interior forest and shrub-steppe all were under logs.

[e] High use of overhanging rocks in interior forest reflects samples from Sheep River (data from DA Boag, pers. comm.); 11/12 under overhanging rocks were from this area. Rocks rarely provided overhead cover in most areas.

leaved herbs, shrubs, small deciduous trees, and rocks were seldom used. In the youngest seres, where conifers were sparse or very small, logs and stumps most often provided overhead cover, but as young conifers grew, they were most used (Table 10.6). This suggests a clear selection for small conifers, if available, as the cover provided by logs and stumps remained more or less constant at 6%–12% between 1962 and 1977 (Table 7.1). Few nests have been found in old-growth or older second-growth (≥30 years post-logging) coast forest. Of eight in our samples, four were backed up to the base of large trees with little or no immediate cover other than that provided by the trunk of the tree (Fig. 10.7), two were under small conifers, one was under a shrub, and one under a log.

Although shrubs seldom provide overhead cover in coast forest, they are heavily used in interior forest and shrub-steppe habitats (Table 10.7). Grasses, mainly large bunchgrasses, and broad-leaved herbs take on added importance in shrub-steppe habitats (Fig. 10.9). Three subalpine nests were all under kruppelholz subalpine fir. Though overhead cover is almost universal at nest sites, kinds vary with availability.

Particular species of plants may be selected as overhead cover from among those with similar growth forms. For example, in northcentral Utah, 14 of 16 nests were under or immediately adjacent to black (*Artemisiia nova*) or big (*A. tridentata*) sagebrush. Only one was associated with black sagebrush, even though it was most abundant (Weber 1975, p. 27).

Protective value of cover varies (Fig. 10.9). It may be very sparse, with hen or eggs in almost complete view, to very dense, with hen or eggs visible only by moving vegetation. Examples of the first were relatively common at Comox Burn in the first 2–3 years after the area was burned. Some hens nested with no overhead cover other than logs or dead twigs and had little protection from potential predators or extreme weather. By the mid to late 1970s, many hens nested under small conifers (Table 10.6) that ranged in height from 0.6 to 6.5 m—mainly plantation trees between 1 and 4 m tall. Many nests were sufficiently hidden that they were found only by pointing dogs or radio-telemetry. Some hens incubated in near complete darkness and almost certainly, in a very different microclimate from that of very exposed nests. Compensation for microclimatic differences likely resides in physiological attributes and behavioural activities of incubating females.

Beyond overhead cover, nests on interior breeding ranges vary from well hidden by herbaceous vegetation, especially large bunchgrasses or broad-leaved herbs, to poorly hidden, the latter especially on overgrazed rangeland. Nest sites may change with growth of vegetation, from barren at time of laying to lush and well concealed at hatch (Zwickel 1992). For information on cover at nest sites as it relates to nesting success see 19.2.4.

(b) *Distance to water.* Availability of free water could be important in nest site selection. We have estimates of distances of nests to free water at three areas. In young coast forest in British Columbia, the median distance of 435 nests from free water was 50 m (2–550 m). At Skalkaho, an interior forest–grassland habitat, median distance of 9 nests was 30 m (7–80 m), and on a shrub-steppe habitat in northcentral Washington, that of 24 nests was 150 m (10–800 m), from free water. In northcentral Utah most nests were located within 0.25 miles [457 m] of free water (Weber 1975). Wide ranges suggest near proximity to free water is not likely to be critical in nest site selection. Relatively succulent foods are usually available in the main nesting season, and free water may be unimportant in nest site selection.

(c) *Distance to brood range.* Females might select nest sites with respect to proximity to brood range. Evidence for such selection is mixed, for some hens move relatively long distances from their nests soon after hatch and establish brood ranges well away from them, while others do not. For example, in the Quinsam area, "Both adult and yearling hens often had nest sites at the edge of, or completely away from, their brood ranges" (Armleder 1980, p. 29). By end of the first week after hatch, yearling brood hens had moved farther from their nests, on average, than adults. Armleder illustrated this relationship for four hens in his Appendix 4. We calculated distances from nests to nearest edge of brood ranges for these birds as follows: one yearling, 1.2 km; and three adults, 0.0 km, 0.0 km, and 0.4 km, respectively. Armleder suggested requirements for nesting are different than for broods.

At Comox Burn, Sopuck (1979) also found some hens with new chicks moving long distances from their nests soon after hatch. He concluded (p. 55), ". . . brood range is not always associated with nest sites . . . ", and, ". . . new recruits [yearlings] may be selecting nest sites in areas not occupied by established hens, rather than for [nearby] brood range . . ." Lance (1967) also suggested pre-hatch home ranges are not selected for later use by hens with chicks.

Clearly, some hens establish brood ranges well away from their nests, and this appears to be more common among, but not restricted to, yearlings. Perhaps nesting home ranges are more keyed into spacing among females (see (d) below) than to resource needs of chicks if acceptable brood range is within the range of mobility of newly hatched young. Unfortunately, we don't know what effect long movements by very young chicks have on their survival.

(d) *Dispersion of nests.* Nests are difficult to find because hens sit tightly.[12] There is only one instance in which all, or virtually all, nests have been found on a given area. Lance (1967) made a special effort to find all nests on ~80 ha of the study area at Comox Burn$_{cp}$ and believes he did so. He found seven, from which he obtained six measurements between adjacent nests; median distance was 251 m (mean = 273 m, range = 161–422 m).[13] He noted, however, that active nests have been found less than 10 m apart. Two were under the same shrub, ~2 m apart (Zwickel 1992). These cases are rare, however, and Lance's data support the suggestion that nests are rarely within 50 m of another (Zwickel 1992). This may reflect spacing of nests among females, but more intensive study of their dispersion is needed (see also 15.3.2 and 17.3.2(a)).

Lance also measured distances from these nests to activity centres of nearest territorial males; median = 80 m (mean = 99 m, range = 80–171 m, $n = 7$), significantly less than nest to nest distances [8]. All were closer to the nearest male than to another nest, leading Lance to suggest that females nest near males with which they breed.

10.5.2 Materials and lining

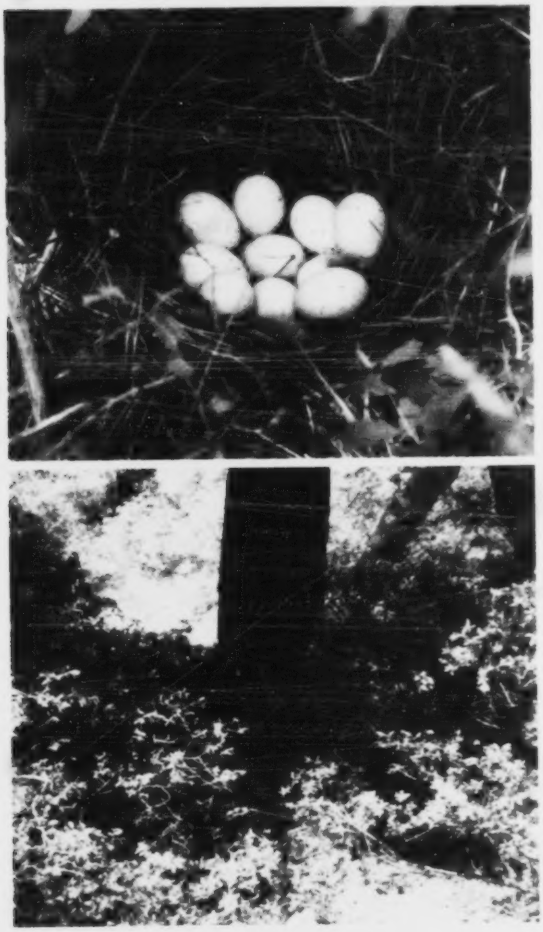
Nests are composed of various amounts of plant material and feathers, usually placed loosely in shallow scrapes in the ground. In Idaho, Caswell (1954*b*) estimated them to be ~17 cm in diameter and 4–5 cm deep. The mean diameter and mean depth of 18 nests on Vancouver Island was 22 ± 0.4 cm (17.8–22.9 cm) and 8 ± 0.6 cm (1.3–12.5 cm), respectively.[14]

(a) *Materials.* Dead plant material from within ~1 m of the nest forms the bulk of its lining and living material is usually avoided.[15] In coastal areas, materials may include small pieces of bark or rotten wood, small twigs, dried moss, dried leaves or needles of species such as grasses, bracken fern, Douglas-fir, western hemlock, salal, fireweed, trailing blackberry, huckleberries (*Vaccinium* spp.), pearly everlasting, and bunchberry. In shrub-steppe habitats, grasses usually dominate the lining, but dried leaves of other herbs or small twigs may be included. One or two materials that appear most available usually dominate within a given nest.

Once incubation begins, most nests include some contour feathers, perhaps from the brood patch of the female. Among 104 nests for which numbers of feathers were counted or estimated, the median number was 20 (mean = 22 ± 1.8); 4 had none and 2 had ±100, the maximum. In general, feathers contribute little to the volume of the lining, although they made up its bulk (±30 only) in one interior nest.

(b) *Lining.* Nest bowls may be well (Fig. 10.10) to poorly (Fig. 7.12) lined. We classified linings as poor, moderate, or good[16] for 158 nests at Comox Burn, 28 at Hardwicke Island, and 14 from interior populations, with no significant difference among areas [9]. Twenty-seven percent were poorly lined, 20% moderately well lined, and 53% well lined. There was no difference between those of yearling (29% poor, 17% moderate, 54% good; $n = 63$) and adult (29%, 22%, 49%; $n = 69$) hens [10], so age and experience of the hen does not seem to determine quality of the lining.

Fig. 10.10. *D.o. sierrae* nest composed almost solely of ponderosa pine needles, ~5 cm thick throughout; very well lined and well hidden. Jumpoff Ridge, Snoqualmie National Forest, WA.



Construction of the nest appears to take place mainly during laying, for there was a significant trend for nests to be less well lined at this time ($n = 15$) than post-laying ($n = 185$) [11]. We found a weak, but significant trend for the quality of the lining to decline as incubation advanced [12], suggesting little material is added once incubation begins.[17]

10.5.3 Microclimate

(a) *Thermal regimes*. There are few data on microclimate at nests. Nevertheless, microclimate must vary widely, for even within areas, nests may have little protection from meteorological elements such as wind, rain, and sun, or be well protected from the elements by dense cover of living or dead (logs or stumps) vegetation. They are found in coastal old-growth forest (cool, humid habitats), xeric shrub-steppe (hot, dry habitats), to subalpine–alpine ecotones (cold habitats: Zwickel 1992).

Table 10.8. Daytime and nighttime, and maximum and minimum, ambient temperatures (t_a; °C) at a Middle Quinsam and a Comox Burn nest.

	Mean temperature[a]		Maximum	Minimum
Area	Day	Night	temp.	temp.
MIDDLE QUINSAM				
25–26 May	19.3	8.2	24.4	4.4
29–30 May	10.5	4.7	14.4	2.2
2–3 June	11.3	4.0	15.6	1.1
COMOX BURN				
5–6 June	17.1	9.7	18.9	6.1
15–16 June	31.6	19.1	38.9	15.0
20–21 June	15.6	11.8	22.8	10.6

[a] Day, 08:00–19:45 h; night, 20:00–07:45 h.

Table 10.9. Mean egg surface (t_e) and nest bottom (t_n) temperatures (°C)[a] at a Middle Quinsam and a Comox Burn nest, by date (observation period). Days of incubation are in parentheses.

	Egg surface	Nest bottom	Difference
MIDDLE QUINSAM			
25–26 May (2, 3)	33.4±0.21	27.1±0.18	6.3
29–30 May (5, 6)	33.0±0.28	22.5±0.13	10.5
2–3 June (9, 10)	32.2±0.16	22.5±0.09	9.7
COMOX BURN			
5–6 June (10, 11)	34.8±0.22	26.8±0.08	8.0
15–16 June (20, 21)	34.1±0.16	33.3±0.13	0.8
20–21 June (25, 26)	34.4±0.21	30.7±0.09	3.7

[a] Female on nest (recess temperatures excluded).

We have data on thermal regimes near and in two nests during incubation, one at Middle Quinsam and one at Comox Burn$_{cp}$. Each was monitored for three 24-h periods with four thermistors: one attached to the surface of one egg (t_e), one at bottom of the nest (t_n), one at surface of the ground outside the nest (t_g), and one to measure ambient temperature near the nest (t_a).[18] Mean, maximum, and minimum ambient temperatures varied greatly, within and between years (Table 10.8).

Within nests, mean t_e values when the Middle Quinsam female was incubating (Table 10.9) varied significantly among observation periods (that on 2 and 3 June was lower than 25 and 26 and 29 and 30 May), but those at Comox Burn did not [13a, b]—maximum difference among means was 2.6°C. Mean t_n values varied significantly and relatively widely among periods at both nests [14a, b] (Figs. 10.11 and 10.12). Relatively stable t_e values and variable t_n values indicated that there were daily variations in thermal gradients between nest bottoms and surfaces of the eggs; i.e., eggs were subjected to different temperature regimes from day to day. Regressions of mean t_e values against mean t_a values and t_g values for each 24-h period were not significant [15a, b]. In contrast, regressions of mean t_n values against mean t_a values and t_g were significant [16a, b]. Thus, variation in mean t_e showed no clear

Fig. 10.11. Temperatures (°C) at surface of one egg, bottom of nest, ground outside nest, and ambient near nest; Middle Quinsam, 25–26 May, 29–30 May, and 2–3 June. Arrows denote known departures of hen from nest.

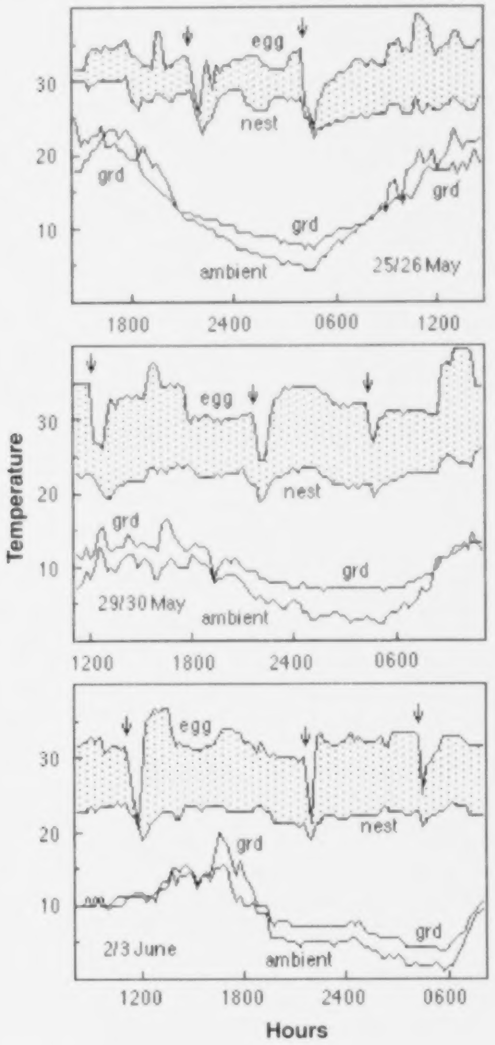
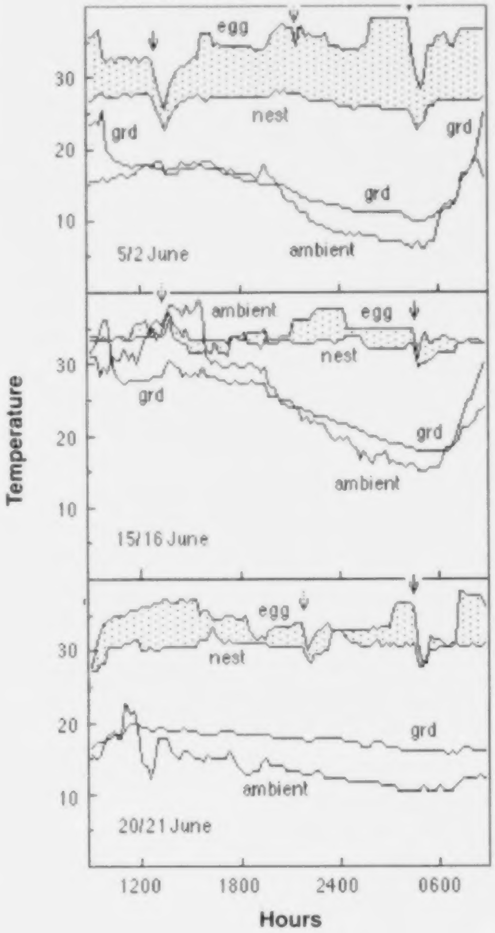


Fig. 10.12. Temperatures (°C) at surface of one egg, bottom of nest, ground outside nest, and ambient near nest; Comox Burn$_{cp}$, 5–6 June, 15–16 June, and 20–21 June. Solid arrows denote known departures of hen from nest; dotted arrows denote likely departures.



relationship to external temperatures, while that for t_n appears to have been influenced by them. These studies were conducted in early coast forest seres and, although they involved two nests only, clearly document daily variations within nests, and potentially, among years. Since blue grouse breed in many different types of habitats and among which climate varies widely, thermal regimes to which eggs are subjected almost certainly differ. Variations within and between nests would affect costs to the hen in keeping eggs at correct temperatures and might affect the viability of developing embryos and subsequent survival of chicks, a subject deserving further study.

(b) *Recesses from nests*. Departure of the female from the nest, a recess, subjects eggs to temporary cooling (Figs. 10.11 and 10.12). Including suspected departures, they ranged from 2 to 3 per 24 hours in our study, a mean of 2.7. We determined lengths of six recesses to the nearest minute at the above nests, and of seven at two other nests. Median length of absences was 22 min (mean = 26 ± 4.5 min, range = 7–65 min). At 3 recesses per 24 hours, a hen would be off the nest about 5% of the total incubation period, similar to other tetraonines (Semenov-Tyan-Shanskii 1960; Lennerstedt 1966; Valanne 1966; Pullianen 1971; Erikstad 1986; Gabrielsen and Unander 1987; Naylor et al. 1988). We suspect lengths and numbers of recesses are geared to maintenance needs of the hen, especially defecation and time to feed, so access to feeding areas may be an important component of nest site selection (see also 17.3.2(b)).

10.5.4 Distance between subsequent nests: within and among years

Within years, second nests (renests) are built only after desertion or destruction by predation of a first clutch. Two (one renest) is the maximum number known for any female within a year. Median distance between first and second nests of 10 banded hens at Comox Burn and Hardwicke Island was 162 m (45–531 m; Zwickel 1992). Six first clutches were destroyed by predation, four were deserted. Median distance between sites of 26 hens whose nests were found in more than 1 year[19] was 174 m (9–1956 m), not different than for renests [17]. Ninety-two percent of first clutches among the latter group hatched, and two suffered from predation. Considering all first and subsequent nests, hens did not move greater distances after predation or desertion than after a successful hatch. We have never seen a nest site used more than once, within or among years.

10.6 Nesting parameters

Principal parameters associated with nesting include length of the incubation period, clutch size, fertility and hatchability of eggs, and nesting success. The most comprehensive data from which to estimate them are from Comox Burn, 1962–1965 and 1969–1978, and Hardwicke Island, 1979–1984. During these periods, breeding density was increasing or stable at Comox Burn and declining at Hardwicke Island. We use data from Comox Burn as a principal basis for examining these factors, but include some data from Hardwicke Island and compare to interior populations where possible.

10.6.1 The incubation period

(a) *Timing*. Exact time when incubation begins is difficult to establish. Our observations indicate, however, that it begins with laying of the last egg, for hens are rarely found off the nest after this time and for short periods only, presumably for feeding and other maintenance activities.

The incubation period of blue grouse has been reported as ranging from 18 (Bent 1932) to 28 (Smith 1962) days, although most reports (Bendell 1954; Caswell 1954*b*; Standing 1960; Smith 1962; Zwickel 1977; and Pekins 1988) centre around 25–26 days. McKinnon and Zwickel (1988) found incubation periods of 25–27 days for five clutches of eggs from Vancouver and Hardwicke islands, with a mean of 25.8 ± 0.2 days. They concluded that most studies (except Bent 1932) suggest a mean incubation period of 26 days for blue grouse,[20] with a variation of ±1 day.

(b) *Extended incubation*. We know of three extended incubation periods. One was induced by us, and two were a result of infertile eggs or dead embryos.

Caswell (1954*b*) was shown a seven-egg nest on 24 May (first found 14 May) on which the female incubated until 4 July, at which time she deserted—41 days after first seen by Caswell.[21] This clutch likely was being incubated on 24 May. The second extended incubation period was by a yearling female at Middle Quinsam. All eggs were taken for aviary studies and replaced by hard-boiled bantam chicken eggs. Beginning of incubation was estimated as 21 May on the basis of date of hatch of eggs in our aviary. The hen was collected from the nest on 19 July, providing an estimated incubation period of 51 days, approximately twice the normal length. The third case involved a nest at Skalkaho. It was found with seven eggs on 26 May. An eighth, final egg was laid on 28 or 29 May, signifying the start of incubation. The hen was last seen on the nest on 4 July, providing an incubation period of 37–38 days. No sign of embryos was found in any of the eggs, all presumably infertile. Extended incubation periods on dead or infertile eggs are well documented for other birds (Sowles 1955).

Despite a double-length incubation period for the female at Middle Quinsam, her body mass of 759 g was not unduly light for a yearling completing incubation. Her brood patch, however, was about one-half filled in, and she was replacing the first three primaries on each wing, neither of which normally occurs until after hatch.[22] In contrast to the normal situation, extended incubation did not suppress her moult.

10.6.2 Clutch size

(a) *Coastal populations*. Mean size of completed clutches of adult females at Comox Burn from 1969 to 1978 was 7.1 ± 0.13, significantly larger than that of yearlings, 5.5 ± 0.13 (Fig. 10.13) [18]. In 10 cases involving the same female as a yearling and as a 2- or 3-year-old (data from Comox Burn and Hardwicke Island), clutch sizes were 2 and 5, 3 and 4, 4 and 4, 4 and 5, 5 and 6, 6 and 7 ($n = 2$), and 7 and 8 ($n = 3$), respectively. Clearly, clutch size tends to increase from 1 to 2 years of age. Smaller clutches in yearlings than adults might reflect either inexperience in foraging, inexperience in obtaining a space, or physiological immaturity. We suspect the latter.

Mean clutch sizes of 2-, 3-, and ≥4-year-old females at Comox Burn and Hardwicke Island (Table 10.10) were not different within areas [19]. Those of 14 adults were determined in 2 or 3 different years (Table 10.11). Size increased in four cases, decreased in four, and did not change in eight, from one nest to the next. Among those that differed among years, five increased or decreased by one egg, one increased by two,

Fig. 10.13. Frequency distribution of clutch sizes (%) of yearling and adult females, Comox Burn, 1962–1978.

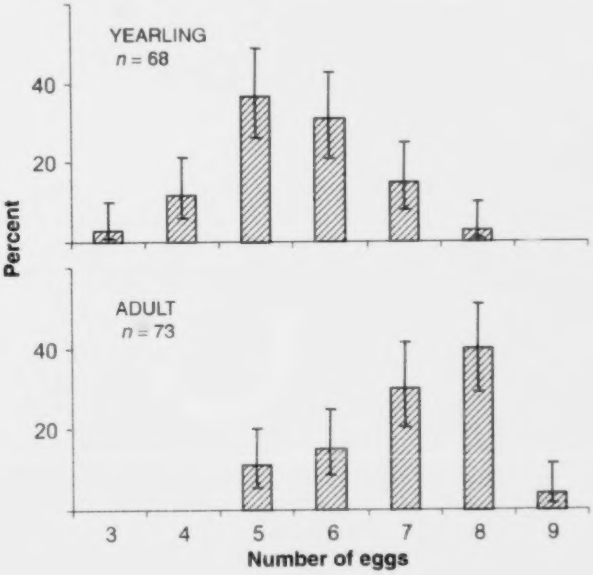


Table 10.10. Clutch sizes (mean ± SE) of 2, 3, and ≥4-year-old females at Comox Burn and Hardwicke Island.

	Comox Burn		Hardwicke Island	
Age (years)	*n*	Clutch	*n*	Clutch
2	20	7.3±0.27	27	5.6±0.17
3	10	6.6±0.43	8	6.3±0.45
≥4	14	7.5±0.17	22	5.9±0.23

Table 10.11. Clutch sizes of banded adult females with nests found in more than 1 year.

	Size of clutch		
Band no.	Nest 1	Nest 2	Nest 3
COMOX BURN			
1163	6 (≥2)	6 (≥3)	
5653	8 (≥2)	8 (≥6)	
5823	5 (2)	8 (3)	
6432	7 (3)	7 (6)	
HARDWICKE ISLAND			
11967	6 (≥2)	5 (≥3)	5 (≥4)
11991	5 (≥2)	6 (≥3)	
11996	5 (≥3)	5 (≥4)	
12271	5 (4)	5 (6)	
12281	6 (≥2)	5 (≥5)	5 (≥6)
12301	4 (≥4)	6 (≥5)	
12449	7 (≥4)	6 (≥5)	
12937	6 (2)	3 (3)	
13313	4 (3)	5 (4)	
13503	8 (2)	8 (3)	

Note: Within years, only first nests are used. Age of female (years) is in parentheses.

one increased by three, and one decreased by three eggs. These data indicate clutch size does not change, on average, beyond 2 years of age. Size at Comox Burn was earlier reported to have varied among years (Zwickel 1975), and a reanalysis of these data with more samples (Table 10.12) was consistent with that result [20].

Clutch sizes have been reported for four other populations in coastal British Columbia (Table 10.13). Breeding density at Lower Quinsam was very high, at Middle Quinsam moderate, and at Ash River, low to moderate and increasing. Bendell and Elliott (1967) concluded that mean clutch sizes were not different in the Middle and Lower Quinsam populations. That for Ash River was intermediate between these two, but the sample was biased downward because of a high proportion of yearlings in the population. Clutch size for all females at Comox Burn likely was not different from any of these populations, although we could not test them statistically. Mean clutches for populations on Vancouver Island ranged between ~6 and 6.3 eggs per hen. In the high-density, declining population at Hardwicke Island, clutch size of adults, 5.8 ± 0.16 (range = 1 to 8, *n* = 65), yearlings, 5.0 ± 0.12 (range = 3–7, *n* = 57), and all females combined (Table 10.13), were significantly lower than at Comox Burn [21a–c].

Table 10.12. Size of clutches[a] at Comox Burn, by year, 1962–1965 and 1969–1978.[b]

	No. of clutches	Mean (±SE)	Range
1962	12	5.8±0.31	4–7
1963	5	6.4±0.75	4–8
1964	14	7.0±0.39	5–9
1965	1	5.0	—
Total, 1962–1965	32	6.4±0.25	4–9
1969	11	5.8±0.46	3–9
1970	9	6.9±0.42	4–8
1971	26	6.4±0.22	4–9
1972	16	6.4±0.43	3–8
1973	26	6.3±0.23	5–8
1974	24	7.2±0.21	5–9
1975	12	6.6±0.38	4–8
1978	3	7.0±0.00	7
Total, 1969–1978	127	6.5±0.11	3–9
Grand total	159	6.5±0.10	3–9

[a] Includes yearlings, adults, and females of unknown age.

[b] Data for 1976–1977 excluded because of a disproportionate number of yearlings in samples owing to telemetry study.

Table 10.13. Size of clutches (mean ± SE) of females[a] in five local populations in coastal British Columbia.

Area	Years	*n*	Mean	Range	Source[b]
Lower Quinsam	1950–1953	6	6.0±0.66	5–7	1
Middle Quinsam	1960–1963	30	6.3±0.35	—	2
Ash River	1969–1971	50	6.1[c]	—	3
Comox Burn[d]	1962–1978	201	6.3±0.11	3–9	4
Hardwicke Island	1979–1984	142	5.4±0.10	1–8	4

[a] Includes yearlings, adults, and females of unknown age.

[b] 1, Bendell (1955*a*); 2, Bendell and Elliott (1967); 3, Redfield (1975); 4, this study.

[c] Standard error not available because data presented as total number of eggs for all clutches.

[d] No data for 1966–1968 and data for 1975–1976 excluded because of a disproportionate number of yearlings in telemetry study.

(b) *Interior populations*. There are no studies of interior races of blue grouse with samples of more than 30 completed clutches. Although sample sizes are relatively small from individual areas, all interior populations with samples of 20 nests or more, except Sheep River, averaged ≥7 eggs per nest (Table 10.14). Information from the literature and our studies for 118 nests of interior females (from Colorado and Nevada to Alberta and British Columbia) show a mean clutch of 7.1 ± 0.15 eggs (range = 2–10),[23] significantly larger than the mean of 6.5 ± 0.10 for females at Comox Burn (Table 10.12) [22]—with a mode of 8 for interior birds and 6 at Comox Burn (Fig. 10.14). The largest mean reported for any population was for *D.o. pallidus* in northeastern Oregon. Most interior birds seem to lay more eggs, on average, than coastal birds.

Table 10.14. Size (mean ± SE) and frequency distribution of clutch sizes from Vancouver Island,[a] southeastern Alberta,[b] northcentral Washington,[c] western Montana,[d] and northeastern Oregon.[e]

	VI	AB	WA	MT	OR
No. of clutches	201	20	30	20	27
Mean	6.3±0.1	6.5±0.4	7.1±0.3	7.2±0.3	7.7±0.3
No. of eggs	Percent frequency distribution				
2	—	5	—	—	—
3	2	—	—	—	4
4	5	—	7	5	4
5	23	15	10	5	4
6	23	35	20	20	4
7	27	15	23	30	15
8	18	25	17	25	41
9	2	5	20	5	18
10	—	—	3	10	11

[a] Data from Comox Burn, 1962–1978.

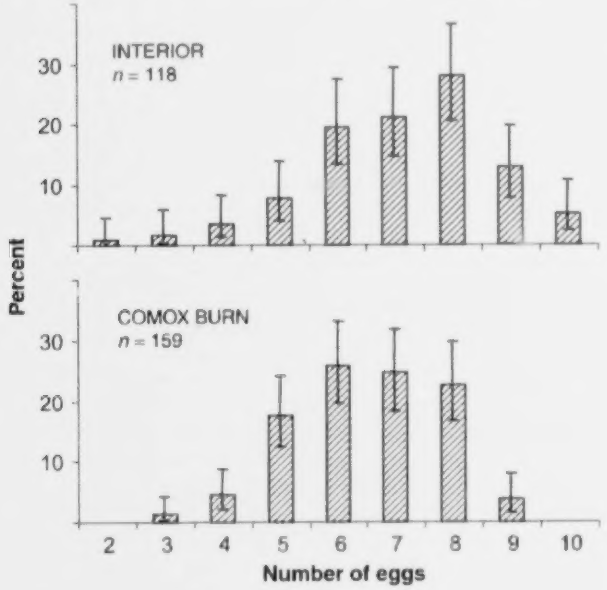
[b] Data from Sheep River (DA Boag, pers. comm.).

[c] Sources: Bauer (1962), M.A. Degner (pers. comm.), Henderson (1960), Jewett et al. (1953), RA Lewis (pers. comm.), Schotellius (1951*a*), MA Schroeder (pers. comm.), E Smith (pers. comm.), Standing (1960), Wing et al. (1940), and this study.

[d] Data from Mussehl (1963*b*, *c*), P Schladweiler (pers. comm.), and this study.

[e] Data from Pelren and Crawford (1999).

Fig. 10.14. Frequency distribution of clutch sizes (%) of interior and Comox Burn females (includes females of unknown age).



(c) *Maximum clutch size*. The largest set of eggs we have seen in the wild is 10, although larger clutches have been reported: up to 15 (Jewett et al. 1953). The largest we have seen, 12 eggs, is at the American Museum of Natural History (AMNH 6831) and was collected in the Wasatch Mountains, UT, in 1899. Bent (1932) suspected reported clutches >12 involved laying by more than one female, and we agree.

(d) *Size of first and second clutches within years*. Data on the distribution of hatch suggest most late broods result from second nesting attempts, so-called renests. Renesting is now well documented in blue grouse (Zwickel and Lance 1965; Sopuck and Zwickel 1983),[24] and second clutches are smaller than first by ~1–1.5 eggs (Zwickel 1992). At Comox Burn, clutches of adults that hatched on or before 30 June (likely first nests (Zwickel 1975)) averaged 7.4 ± 0.14 eggs (n = 55 nests), significantly larger than those hatched after this date (likely renests), 5.7 ± 0.23 (n = 15) [23a]. Clutches of yearlings hatched on or before 5 July (likely first nests (Sopuck 1979)) averaged 5.6 ± 0.16 eggs (n = 42 nests), not larger than those hatched after this date, 4.5 ± 0.29 (n = 4) [23b], but approaching significance. Lack of a difference may relate to the small sample of late nests. In four cases we determined size of clutch of first and second nests of individual females within years. Three adults had clutches of 5 and 4, 7 and 5, and 8 and 6, and one yearling, 6 and 5, in first and second nests, respectively. Second clutches are clearly smaller, on average, than in first nests.

10.6.3 Fertility of eggs[25]

(a) *Coastal populations*. Early data on fertility of eggs of yearling and adult females at Comox Burn indicated no difference between age classes (Zwickel 1975). Larger samples (Table 10.15) also were not different [24]. Yearlings and adults appear equal at producing fertile eggs.

Nine years of data on egg fertility of females at Comox Burn (Table 10.16) showed a significant difference among years [25a]. When data for the 2 years with lowest fertility, 1971 and 1974, were deleted, there was no difference among the other years [25b]. Contrary to Zwickel (1975), fertility may vary among years. Nevertheless, it always equaled or exceeded 92%, and including all years, averaged 96%.

Data from Hardwicke Island showed no difference in egg fertility between yearlings and adults or among years (Zwickel et al. 1988). A fertility of 93% for all females and years,

Table 10.15. Fertility and hatchability of eggs of yearling and adult females at Comox Burn, 1969–1978.

	Age of female	
	Yearling	Adult
FERTILITY		
No. of clutches	48	55
No. of eggs	209	356
Percent fertile	96	97
HATCHABILITY[a]		
No. of clutches	42	53
No. of eggs	193	341
Percent hatched	92	94
No. of fertile eggs	174	325
Percent hatched	97	97

[a] Includes only eggs of hens successful in completing incubation.

Table 10.16. Fertility and hatchability of eggs[a] at Comox Burn by year.

	1969	1970	1971	1972	1973	1974	1975	1976	1977
FERTILITY									
No. of clutches	8	5	22	9	19	15	9	13	22
No. of eggs	43	16	145	55	93	110	35	49	115
Percent fertile	98	100	94	98	100	92	100	98	96
HATCHABILITY[b]									
No. of clutches	8	2	22	9	17	12	9	10	22
No. of eggs	43	10	144	55	89	89	35	44	112
Percent hatched	95	100	92	93	99	91	100	89	88
No. fertile eggs[c]	42	10	135	54	89	83	35	34	98
Percent hatched	98	100	98	94	99	97	100	97	95

[a] Includes eggs of yearlings, adults, and females of unknown age.

[b] Includes only eggs of hens successful in completing the nesting cycle.

[c] 109 clutches only.

however, was significantly lower than at Comox Burn. Thus, fertility may differ among local populations in the same general region.

(b) *Interior populations*. Few data are available on egg fertility for interior birds, and no single sample is adequate for comparative purposes. Nevertheless, combined data from our studies and the literature ($n = 224$ eggs, 38 nests—34 from *D.o. pallidus*) show a fertility of 90%, significantly lower than at Comox Burn [26a], but not different than at Hardwicke Island [26b]. Relatively low fertility of these interior eggs may reflect our sample from Skalkaho where two nearby nests had 13 of 14 eggs infertile, more than one-half of all infertile eggs ($n = 23$). Perhaps there was an infertile male in the immediate area. This may reflect a sample size problem.

10.6.4 Hatchability of eggs

(a) *Coastal populations*. As with fertility, there was no difference in gross hatchability or hatchability of fertile eggs between yearling and adult females at Comox Burn (Table 10.15) or Hardwicke Island (Zwickel et al. 1988). The two age classes appear equal in this respect.

Differences in hatchability can reflect either fertility of eggs or viability of embryos. There were significant differences among years at Comox Burn (Table 10.16) [27a]. In 1971 and 1974 (low fertility) and 1976 and 1977 (normal fertility) hatchability was lower than the other 5 years, which were not different among themselves [27b]. These data suggest a share, at least, of annual differences resulted from embryonic viability, i.e., in 1976 and 1977. There were no differences in hatchability, or that of fertile eggs, among years at Hardwicke Island (Zwickel et al. 1988). That for all years at Comox Burn, 93% ($n = 645$ eggs, 118 clutches), was greater than for all years at Hardwicke, 85% ($n = 793$ eggs, 155 clutches) [28]. Among clutches, all eggs hatched in 80% of 99 clutches at Comox Burn but in only 47% of 155 at Hardwicke, a highly significant difference between areas (Zwickel et al. 1988). Hatchability can vary among populations.

(b) *Interior populations*. Among 434 eggs (58 clutches) examined by us from throughout the range of interior birds, 87% hatched, significantly lower than at Comox Burn [29a], but not different than at Hardwicke Island [29b]. Among 194 fertile eggs (36 clutches) from interior races, 97% hatched, not different from those at Comox Burn or Hardwicke [30a, b]. Since fertility of interior eggs was lower than at Comox Burn, but hatchability of fertile eggs the same, lower hatchability in the interior may reflect mainly infertility.

10.6.5 Nesting success

A successful nest is one in which at least one chick hatched. Nesting success is most often calculated from numbers of nests found ("observed nesting success" (Mayfield 1961)), which, as pointed out by Mayfield, is not necessarily the same as numbers of nests built; e.g., some clutches may be destroyed before being found. We first examine observed nesting success for birds at Comox Burn and Hardwicke Island for comparison to other studies that have not been, or cannot be, corrected in the manner suggested by Mayfield.

(a) *Coastal populations*. Observed nesting success of yearling and adult females (Table 10.17[26]) did not differ at Comox Burn or Hardwicke Island (Zwickel et al. 1988). Again, age classes appear equal.

Nesting success varied significantly among years at Comox Burn, but not at Hardwicke Island (Table 10.18) [31a, b]. Fluctuations at Comox Burn appear to have been caused by small samples, for when data for years for which sample sizes were <10 are deleted, there was no difference, though the data approached significance [31c]. If the significant differences result from small samples, there may be little difference among years.

Observed nesting success for all years combined at Comox Burn (Table 10.18) was significantly lower than at Hardwicke Island [32]. Failure to hatch was caused mainly by predation. Fifty-nine of 61 clutch losses at Comox Burn (97%) and 10 of 11 at Hardwicke (91%) were caused by predators, the remainders by desertion. Most predation appears to have been caused

Table 10.17. Observed nesting success[a] of yearling and adult females at Comox Burn, 1969–1978, and Hardwicke Island, 1979–1984.[b]

	No. of nests	No. hatched	No. lost to predators	No. deserted	Percent hatched
COMOX BURN					
Yearling	25	23	2	0	92
Adult	56[c]	48	7	1	86
HARDWICKE ISLAND					
Yearling	21	19	2	0	91
Adult	41	39	2	0	95

[a] Includes all nests in which at least one egg hatched.

[b] Samples from females with radios excluded, as radios may affect the calculation of observed nesting success (Sopuck 1979).

[c] This figure was reported incorrectly as 66 in Zwickel et al. (1988), but this correction does not change the conclusion reported there.

Table 10.18. Observed nesting success[a] of all females[b] by year at Comox Burn and Hardwicke Island[c].

	No. of nests	No. hatched	No. lost to predators	No. deserted	Percent hatched
COMOX BURN					
1969	10	7	3	0	70
1970	7	2	5	0	29
1971	26	21	5	0	81
1972	16	8	8	0	50
1973	26	17	9	0	65
1974	26	14	10	2	54
1975	10	9	1	0	90
1976	8	2	6	0	25
1977	12	5	7	0	42
1978	5	0	5	0	0
Total	146	85	59	2	58
HARDWICKE ISLAND					
1979	20	18	1	1	90
1980	12	12	0	0	100
1981	22	18	4	0	82
1982	15	12	3	0	80
1983	1	1	0	0	100
1984	7	5	2	0	71
Total	77	66	10	1	86

[a] Includes all nests in which at least one egg hatched.

[b] Includes yearlings, adults, and females of unknown age.

[c] Nests of females with radios excluded, as radios may affect the calculation of observed nesting success (Sopuck 1979).

by mammals (see 19.2.1), and the difference in nesting success between Comox Burn and Hardwicke was likely related to differences in the complements of predators on the two areas. The few natural desertions (3/223, <2%) may be the result of females having been killed while away from their nests. Desertion is rare except when observer induced, and when found, occurs mostly in the first half of the laying period (Zwickel and Carveth 1978). In another Vancouver Island population, Ash River, observed nesting success (68%, data in Redfield 1975) was not different than at Comox Burn [33a], but significantly less than at Hardwicke Island [33b].

(b) *Interior populations*. Data on nesting success of interior populations are few. Only five studies involved 10 or more nests (Table 10.19). There was no significant difference among interior populations [34a], and when combined they showed a success rate of 74%, higher than at Comox Burn, but not different from Hardwicke Island [34b, c]. Clearly, there are

Table 10.19. Observed nesting success[a] of all females[b] at Comox Burn, 1969–1978, and Hardwicke Island, 1979–1984, as compared to that at Ash River and five interior populations.

	No. of nests	No. hatched	No. lost to predators	No. deserted	Percent hatched
Hardwicke Island	77	66	10	1	86
Ash River[c]	46	34	?	?	74
Comox Burn	146	85	59	2	58
Sheep River[d]	21	17	2	2	81
Methow Valley	14	9	5	0	64
Green Mt.[e]	10	8	1	1	80
Skalkaho	14	10	3[f]	1	71
Miller Ridge[g]	27	20	?	?	74

[a] Includes all nests in which at least one egg hatched except those of females with radios, which may affect the calculation of observed nesting success (Sopuck 1979).
[b] Includes yearlings, adults, and females of unknown age.
[c] From Redfield (1975).
[d] From Boag (1966).
[e] From Hoffman (1981).
[f] Two nests were destroyed, and one hen died while away from nest.
[g] From Pelren and Crawford (1999).

variations among areas, variations that may relate to densities of grouse populations, diversity and densities of predators, local habitat structure, or some combination of these factors.

(c) *Nesting success corrected as per Mayfield.* Mayfield (1961) suggested that observed nesting success should be corrected to more closely approximate the true situation. We used his method to correct our data for Comox Burn and Hardwicke Island, the two largest samples. This analysis suggested nesting success was ~10% less than indicated by uncorrected data (Table 10.20). Corrected nesting success at Comox Burn, 45%, was very similar to a relatively unbiased estimate of 47% for radio-equipped birds on this area (Sopuck 1979).

A further attribute of Mayfield's method is that one can partition nest destruction (the inverse of success) between the laying and incubation periods. Our data indicate that most destruction occurred during incubation (Table 10.20), when the hen spends most of her time on the nest.

Table 10.20. Nesting success (%) calculated by the "observed" and Mayfield (1961) methods[a] at Comox Burn and Hardwicke Island.

		Mayfield		
	Observed	During laying	During incubation	Total
COMOX BURN (1969–1978)	58	93	49	45
HARDWICKE ISLAND (1979–1984)	86	100	75	75

[a] Includes all nests in which at least one egg hatched except that a few used in each method could not be used in the other. Nests of females with radios were excluded because they may affect the calculations (Sopuck 1979).

10.7 Synthesis

The reproductive season of blue grouse begins with gonadal recrudescence, when birds are in winter habitat. Movement to summer habitat (or range) is likely elicited by early stages of recrudescence or something that elicits movement and recrudescence, perhaps increasing temperatures and (or) photoperiod.

The typical breeding pattern involves a rapid rise in numbers of birds breeding to a 2-week-long peak that begins ~3 weeks after first copulations. This is followed by a rapid decline, with a tail that may extend out to 6 weeks beyond the peak, much of which presumably reflects renesting. Pattern of breeding may differ among areas, depending on nesting success and timing of the local season. Time of breeding is area specific and may vary among years on a given area, likely related to seasonal phenology.

Most yearling males presumably do not breed, but pass through all stages of spermatogenesis and have fertilized eggs in the aviary. In contrast, many yearling females breed, but the proportion may vary among years and areas. Yearling females differ from adult females in two main ways, by breeding later, or not at all, and by producing fewer and smaller eggs.

Nests, and the immediate site, are a critical part of the environment of breeding females and their eggs. Virtually all have some overhead cover, and are almost always on the ground. They are rarely within 50 m of another, suggesting social constraints may affect their dispersion.

Nests are usually formed in shallow scrapes in the ground and may have almost no other structure, or be well lined. Owing to wide variations among nest sites and their structures, variations are almost certainly compensated for by the hen.

At both Comox Burn and Hardwicke Island, mean clutch size does not appear to vary much among years, but some annual sample sizes are relatively small. Although egg fertility and hatchability may vary among years, it has always exceeded 89% and 84%, respectively, at these areas. Variations in hatchability may result from differences in fertility and (or) viability of embryos.

On average, clutch size is larger in interior than coastal populations. Available data suggest egg fertility and hatchability, however, may be lower in interior than coastal populations. Nesting success differs substantially among populations and may be related to differences in densities of the grouse populations, diversity and densities of nest predators, local habitat structure, or two or more of these combined.

At Hardwicke Island, a declining population, clutch size and egg fertility and hatchability were all lower than at nearby Comox Burn, an increasing or stable population. The high-density population at Hardwicke Island had higher nesting success, however, apparently a result of the small island and fewer predators. These examples suggest grouse density and the local environment may affect clutch size and fertility and hatchability of eggs.

Endnotes [Chapter 10]

1. Breeding events were calculated as follows: (1) hatch dates were determined by back-dating from age of captured chicks (Zwickel and Lance 1966; Redfield and Zwickel 1976) or from hatch dates of nests; (2) beginning of incubation was extrapolated backwards from hatch dates on the basis of a 26-day incubation period (McKinnon and Zwickel 1988); (3) rate of egg-laying has been reported as 1.5 days/egg (Caswell 1954*b*; Standing 1960); we used this and a mean clutch of six eggs to extrapolate first egg dates from beginning of incubation; and (4) no data exist on time from copulation to laying of the first egg for blue grouse, but Bump et al. (1947, p. 167) reported 3–7 days for female ruffed grouse, and Svedarsky (1988), 4 days for greater prairie-chickens; we used 4 days to backdate from first egg to time of copulation. A clear 2-week mode, the "peak", is usual in annual samples of hatch dates—>60% of the hatch occurred in this period in 16 of 19 years for which we have data. We consider this mode for each event as its "peak".

2. Sources of data for Fig. 10.3 are Bendell (1954), Caswell (1954*b*), Mussehl (1958), Henderson (1960), Standing (1960), Bauer (1962), Boag (1966), Mussehl and Schladweiler (1967), King (1971), Harju (1974), Weber (1975), Hoffman (1981), Cedarleaf et al. (1982), Crawford et al. (1986*a*), and our studies at Duck Creek, the May Ranch, Skalkaho, and in British Columbia.

3. Hoyt showed that a volume constant (K_V) of 0.51 applies to most bird eggs, and this was used to compute egg volumes. He reported that mass constants (K_W) are species specific. We computed a mean K_W of 0.528 from 35 fresh eggs and used this value to estimate fresh mass. Mean fresh mass of these eggs, 34.4 ± 0.57 g, did not differ from a predicted mean of 34.5 ± 0.52 g, calculated with this K_W.

4. No difference in any mean between eggs from Vancouver and Hardwicke islands.

5. Loss of water in the last day or two prior to hatch may exceed that for earlier periods because the shell is partially opened during pipping, and the chick is very active.

6. Warren noted that a temperature dependent reduction in egg size is expressed mainly in the white and eggshell, less in the yolk.

7. The source of Johnsgard's measurements is unclear, and he used a generalized K_W of 0.552 to calculate fresh mass, as suggested by Stonehouse (1966). A K_W of 0.528, as we calculated for blue grouse and applied to Johnsgard's measurements, gives a mass of 31.4 g.

8. Three measurements of each eggshell, membranes excluded, were used to compute a mean value for that egg, using the technique of Lewin (1970). Measurements were taken near the hatch line on the pointed end of shell remains.

9. At one nest not included in this analysis, 9 days separated laying of the fifth and sixth eggs, with a final clutch of eight. Differences in colour between the first five and last three eggs indicate this clutch was laid by two hens.

10. Although our data suggest laying rate on our area may be 2 days/egg, we used 1.5 as reported by Standing and for most grouse by Johnsgard. If it really is 2 days, timing of copulation and first eggs would be 2.5 days earlier than depicted in Fig. 10.1 but would not change the general picture.

11. Mean May body mass of females is less than maximum (Endnote 1, Chap. 9), resulting in overestimates of these parameters as percentages of maximum body mass.

12. Until extensive use of dogs in the late 1950s and introduction of radio-telemetry in the mid 1960s only scattered nest records were available.

13. Seven nests on 80 ha equates to 41 on the entire 465-ha study area. This is well within what might be predicted with the breeding density at the time. It is consistent with Lance's contention that he found all nests on that subsection of Comox Burn.

14. Nest measurements are subject to some error because the exact edge of the nest bowl requires subjective judgment. Our measurements were to the outer limits of nests, Caswell's may have been diameter of the bowl. Depths may vary with characteristics of the substrate.

15. One nest in coastal British Columbia was on a bed of live moss.

16. Poor, little nest material, offering poor cushioning and insulation for eggs, often incomplete coverage of soil; good, good cushioning for eggs, ±2.5 cm thick lining, no exposed soil in nest bowl; moderate is intermediate between these extremes.

17. The negative trend may be explained in part because post-laying nests include some that were described after hatch or destruction by predation, with some nest material perhaps removed by scavengers, predators, or wind prior to write-up.

18. Temperatures were recorded at 15-min intervals with a telethermometer. Thermistor t_e was free to roll with the egg and subject to shifting by the female; t_n was exposed to the eggs and immobilized at centre of the nest bottom; t_g was immobilized <2 cm under soil or litter ~10–15 cm from edge of the nest bowl; and t_a

was exposed to air in the shade within ≤3 m of the nest. The Middle Quinsam clutch was lost to predation between 3 and 6 June.

19. Twenty-one pairs were year-to-year nests, five ranged from 2 to 4 years between first and subsequent nests.

20. This conclusion was based on data representing 13 clutches and four subspecies of blue grouse, coastal and interior, and as determined in the aviary (5 clutches) and the wild. We now have data from a fourteenth nest in the wild that had a 26-day incubation period.

21. Eggs were apparently not examined for fertility or dead embryos.

22. This hen's moult score (Zwickel and Dake 1977) was about equal to that of a female with 10-day-old chicks.

23. Clutch sizes, hatchability, and fertility for interior subspecies were compiled from the following: Bent (1932), Boag (1966), Caswell (1954*b*), Heebner (1956), Hoffman (1981), Jewett et al. (1953), Mussehl (1962, 1963*c*), Pelren and Crawford (1999), Schottelius (1951*a*), Schladweiler (pers. comm.), MA Schroeder (pers. comm.), E Smith (pers. comm.), Standing (1960), Weber (1975), Wing et al. (1940), and our studies at Duck Creek, Skalkaho, and Hudson Bay Mt.

24. Data from radio-equipped females at Comox Burn indicated that most adults, but few yearlings, whose first nests were destroyed or deserted attempted to renest (Sopuck and Zwickel 1983). In adults, at least, second nests may be started even when a first nest is destroyed late in incubation, and within 15 days or less after destruction (Zwickel and Lance 1965).

25. Eggs with clear visual evidence (by unaided eye) of embryonic growth were classified as fertile, those with no such evidence, as infertile. This minimizes estimates of fertility if embryos in very early stages of development were not detected.

26. Nest success of known-aged hens is higher than for "all birds" because ages of nest hens were often determined only at, or near, time of hatch.

CHAPTER 11

Growth and Development

> *Life cannot be fully accounted for without an understanding of its dynamic nature, . . .*
>
> BI Balinsky (1960)

As with other galliforms, juvenile blue grouse grow rapidly, a necessity for species with precocial young. Developmental processes do not all proceed at the same rate, however, and are presumably adapted to functional changes selected for by the environment. We use data from several sources, alone or in combination, to examine the growth and development of young.[1]

11.1 Body mass[2]

11.1.1 Mass at hatch—day 1

Chicks at Comox Burn, Middle Quinsam, and Ash River hatch at a mean mass of ~26 g (Table 11.1). Those from these populations seem equivalent in this respect.

Mass at Comox Burn did not fit a normal distribution on day 1 (Fig. 11.1) [1], but by day 2 all data sets there were normal. Perhaps some chicks at the low end of the distribution die quickly? In contrast to chicks from different populations on Vancouver Island, 15 *D.o. fuliginosus* from the May Ranch were significantly lighter than at Comox Burn [2a].

Wing et al. (1944, p. 437) estimated day-old mass of *D.o. pallidus* as 20 g on the basis of "data from other sources", similar to our results in the Methow Valley (Table 11.1). These birds, and those at Skalkaho, were lighter than those at Comox Burn [2b, c]. Seven *D.o. pallidus* from northcentral Washington hatched in an aviary in 1960 (two broods) averaged 18.4 g, and eight from the same population in 1961 (one brood), 16.4 g (Smith and Buss 1963). The only other data for an interior subspecies are those from Duck Creek. Chicks there were lighter than those at Comox Burn [2d], but heavier than those at Skalkaho or the Methow Valley [3a, b]. Newly hatched chicks from Vancouver Island were clearly largest among those for which data are available.

Mean mass of new chicks at Comox Burn was ~71% of that of fresh eggs there, and ~84% of that of eggs at hatch (based on a 15% loss in egg mass during incubation). Mass of chicks at Skalkaho was ~67% of fresh egg mass and ~80% of egg mass at hatch. Remainders reflect the eggshell and its membranes plus nitrogenous wastes and residual water on the shell or evaporated from the newly hatched chick.

11.1.2 The first week of life

(a) *Growth*. Redfield (1978, p. 58) suggested that chicks show little, or no, growth (gain in mass) for the "first few days following hatching", and Van Wagner (1983) reported no growth in the first week of life. At 7 days, however, chicks at Comox Burn averaged 32.6 ± 0.3 g (n = 144, 1973–1978), a 26% increase over day 1. Chicks do grow in their first week of life.

Mean mass of chicks at Comox Burn on day 2, 25.9 ± 0.1 g (n-= 280), was not significantly different than on day 1 [4], indicating little change (Fig. 11.2) [5]. However, mass increased significantly each subsequent day, up to day 5 [6]; at a mean rate of 1.4 g/day.

(b) *Residual yolk*. Egg yolk supplies the principal source of nourishment for the embryo and comprises a diminishing portion of egg mass throughout incubation. Shortly before hatch, the yolk sac (including unused yolk) is drawn into the body by the abdominal muscles. In the domestic chick (*Gallus* sp.) the yolk is "used up" within ~5 days post-hatch (Bellairs 1960, p. 180).

We examined 80 wild chicks of 1–10 days of age for residual yolk, plus many beyond 10 days. The yolk sac and its contents (mean wet mass = 4.4 ± 0.3 g, n = 8) accounted for ~17% of body mass of day-old chicks, ~3% of body mass of 3-day-old chicks, and less than 1% of body mass of 5-day-old chicks. On average, by 3 days of age, chicks had used ~82% of the yolk present on day 1.[3] Clearly, most residual yolk is used in the first 5 days of life, although trace amounts were found in birds up to 9 days of age.[4] Change in mass of the yolk and yolk sac in the first 5 days of life (Fig. 11.2) [7] closely parallels that described for the capercaillie (Marcstrom 1960[5]) and is consistent with that reported by Bellairs (1960) for the domestic chicken.

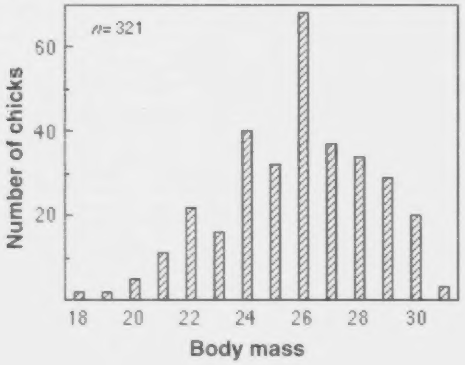
The range in mass of yolk and yolk sacs of individuals was relatively wide at 1 and 2 days of age (3.2–5.7 g, n = 8; and 0.7–4.0 g, n =13, respectively). Some of this variation likely reflects that we did not know precise hatch times, combined with the rapid utilization of yolk at these ages. It is tempting to speculate that amount of residual yolk might relate to subsequent survival in the first days of life, a period when mortality can be high (Zwickel and Bendell 1967*b*), a subject worthy of further study.[5]

Table 11.1. Mean body masses (g) of chicks at hatch[a] among populations.

Area	*n*	Mean ± SE	Range	Subspecies
Comox Burn (field)	321	25.8±0.14	18–31	*fuliginosus*
Comox Burn (aviary)	95	25.5±0.17[b]	20–29	*fuliginosus*
Middle Quinsam	86	26.3[c]		*fuliginosus*
Ash River	78	26.3[d]		*fuliginosus*
May Ranch	15[e]	21.5±0.42	19–25	*fuliginosus*
Methow Valley	12[f]	20.3±0.46	18–25	*pallidus*
Skalkaho	43	19.4±0.26	16–23	*pallidus*
Duck Creek	15[e]	22.7±0.27	21–24	*oreinus*

[a] Mass on day 1.
[b] 1962–1964.
[c] Mean of seven annual means, 1970–1978; calculated by us from Appendix 9 of Van Wagner (1983).
[d] Mean of three annual means, 1969–1971; calculated by us from data in Redfield (1978).
[e] Data from two broods only.
[f] Data from four broods and includes four 2-day-old chicks.

Fig. 11.1. Frequency distribution of body mass (g) of chicks at hatch, Comox Burn, 1973–1978.



11.1.3 The first 13 weeks of life, Vancouver Island

Our field seasons usually encompassed the first 10–12 weeks of life. Examination of birds shot by hunters allowed us to determine sex, age, and mass for birds up to 13 weeks or more. We use mean weekly body mass for birds handled in summer and those killed by hunters to describe changes during this period.

Mass of males at Comox Burn began to clearly diverge from that of females at ~3 weeks of age (Fig. 11.3) [8a, b]. From 1 to 7 weeks of age, however, only in week 4 were males and females significantly different [9]. This may result from several small samples in this period, for weekly means for males exceeded those for females throughout this time. From 8 weeks on, weekly means were all significantly different between the sexes [10a–f].

At 1–2 days of age, males at Comox Burn averaged 26.7 ± 0.4 g ($n = 36$), and females, 25.7 ± 0.4 g ($n = 38$), not quite different [11]. From a mass at hatch of ~26 g, those at week 13 were 898 ± 18.0 g ($n = 7$) and 688 ± 16.4 g ($n = 19$) for males and females, respectively. Mean masses of yearling males and females in early spring (1–15 April), as they came onto breeding range at Comox Burn, were 1104 ± 13.3 g ($n = 24$) and 860 ± 20.4 g ($n = 13$), respectively. Thus, by 13 weeks, chicks had attained ~80% of early spring mass in both sexes. Females were 77% that of males, approximately the same as in yearlings in early spring (78%), and as in yearlings and adults in Washington State in autumn (75%–78% (Zwickel et al. 1966)).

Fig. 11.2. Mean daily body mass (g ± SE) at Comox Burn, 1969–1978, and mean mass of residual yolk (including yolk sac) of chicks 1–5 days old at Comox Burn, 1969–1978, and Hardwicke Island, 1979–1984. Data for areas combined.

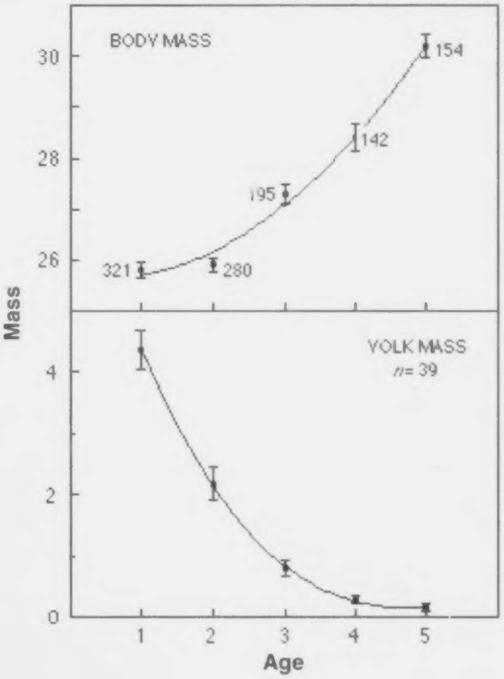
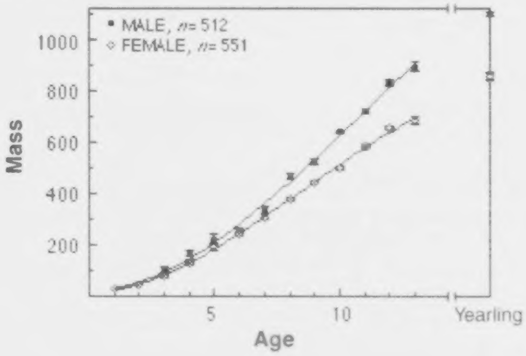


Fig. 11.3. Mean weekly body mass (g ± SE) of juveniles 1–13 weeks of age at Comox Burn, 1969–1978. Mean early spring body masses of yearlings are on right vertical axis.



In absolute terms, weekly gain in mass increased steadily up to ~10 weeks of age in males, and to ~8 weeks of age in females, following which it levelled off and declined (Fig.

11.4) [12a, b]. Expressed as a percent of the previous week's mean, growth rate declined in both sexes from weeks 2 to 13 (Fig. 11.4) [13a, b]. Photos of Smith and Buss (1963) illustrate the rapid changes that occur in the first 16 weeks of life (Fig. 11.5).

Bendell (1955*b*), at Lower Quinsam, provided the first growth curves for young blue grouse. Methods for estimating age of chicks were not available, and he calculated ages from a date of peak hatch (15 June). His curves for males and females were generally similar to those from Comox Burn (Fig. 11.3). By 14 weeks of age, males were significantly heavier than females, but few samples were available for birds of 9–14 weeks. At 15 weeks, males weighed 885 g, females 725 g, less than for yearling males and females, respectively, in spring and summer. Calculated throughout the growth period, males gained 8.57 g/day (60 g/week), females 7.14 g/day (50 g/week).[6]

Redfield (1978) examined growth of chicks in the Ash River Valley during four growth periods: 1–7, 8–15, 16–29, and ≥30 days of age. He could not identify sex of birds <30 days of age and provided data on growth rates of males and females in the fourth period only. Data from Comox Burn, analysed as his, were essentially the same as at Ash River (Table 11.2).

11.1.4 Interior grouse

Wing et al. (1944) collected a small sample of juvenile *D.o. pallidus* in northcentral Washington. Like Bendell (1955*b*), they estimated ages on the basis of a date of peak hatch (1 June). Calculated throughout the growth period, males gained an average of 9.4 g/day (66 g/week), females 8.4 g/day (59 g/week). A similar analysis for *D.o. pallidus* from westcentral Montana, but with a more precise technique for estimating age, showed gains of 10.9 g/day (76 g/week) for males and 8.9 g/day (62 g/week) for females (Schladweiler 1974). Data from both studies suggest more rapid growth than calculated for *D.o. fuliginosus* by Bendell (1955*b*).

Schladweiler (1974) developed growth curves for wild *D.o. pallidus* (Fig. 11.6) [14a–c]. At equivalent ages beyond ~5 weeks of age, *D.o. pallidus* from Montana tended to be heavier than *D.o. fuliginosus* at Comox Burn (compare to Fig. 11.3). By 13 weeks, males and females appeared to be approaching an asymptote, though such tendency was indicated only weakly at this age at Comox Burn. Since *D.o. pallidus* are smaller at hatch than birds at Comox Burn, their rate of growth must be more rapid, consistent with generalized growth rates of birds from the two areas as discussed above.

Young *D.o. pallidus* from northcentral Washington were raised in an aviary by Smith and Buss (1963). Two broods in 1960 had growth curves (male and female) similar to those for *D.o. pallidus* in Montana, but a brood raised in 1961 grew more slowly. Smith and Buss compared body masses of these birds to wild grouse in northcentral Washington and reported that the captive grouse of 1960 approximated more closely the weight of wild grouse than the captive birds of 1961. They thought the difference between years was mainly a result of differences in the kinds of food fed to the aviary birds.

Fig. 11.4. Mean weekly gain in body mass (g) and weekly change (%) in body mass of juveniles at Comox Burn, 1969–1978.

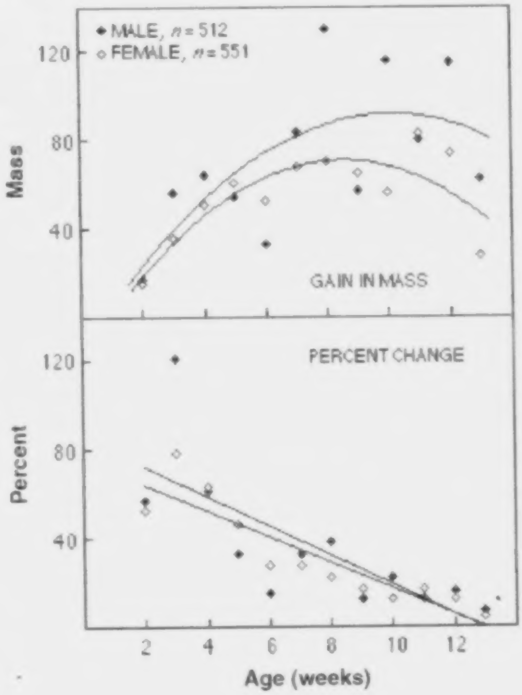


Table 11.2. Growth rate (GR) of chicks expressed as mean body mass gained per day (g) in four growth periods at Comox Burn and Ash River.

	Comox Burn		Ash River[a]		
	Males	Females	Sex?	Males	Females
1–7 days of age					
n	15	21	554		
GR	1.6	1.1	1.2		
SE	0.5	0.4			
8–15 days of age					
n	5	19	261		
GR	2.4	3.0	3.5		
SE	1.1	0.5			
16–29 days of age					
n	10	18	93		
GR	7.9	7.0	8.0		
SE	1.1	1.0			
≥30 days of age					
n	490	494		40	68
GR	13.1	9.6		12.8	10.8
SE	0.3	0.2			

Note: Samples for all years combined at each area.
[a] Data from Redfield (1978).

Fig. 11.5. Plumage and development are useful for determining age of chicks. A, 1 day old; B, 2 weeks; C, 3 weeks; D, 4 weeks; E, 5 weeks; F, 6 weeks; G, 7 weeks; H, 8 weeks; I, 9 weeks; J, 10 weeks; K, 11 weeks; L,12 weeks; M, 13 weeks; N, 14 weeks; P, 15 weeks; R, 16 weeks. Adapted from Fig. 6 of Smith and Buss (1963), courtesy of The Wildlife Society (copyright by The Wildlife Society).

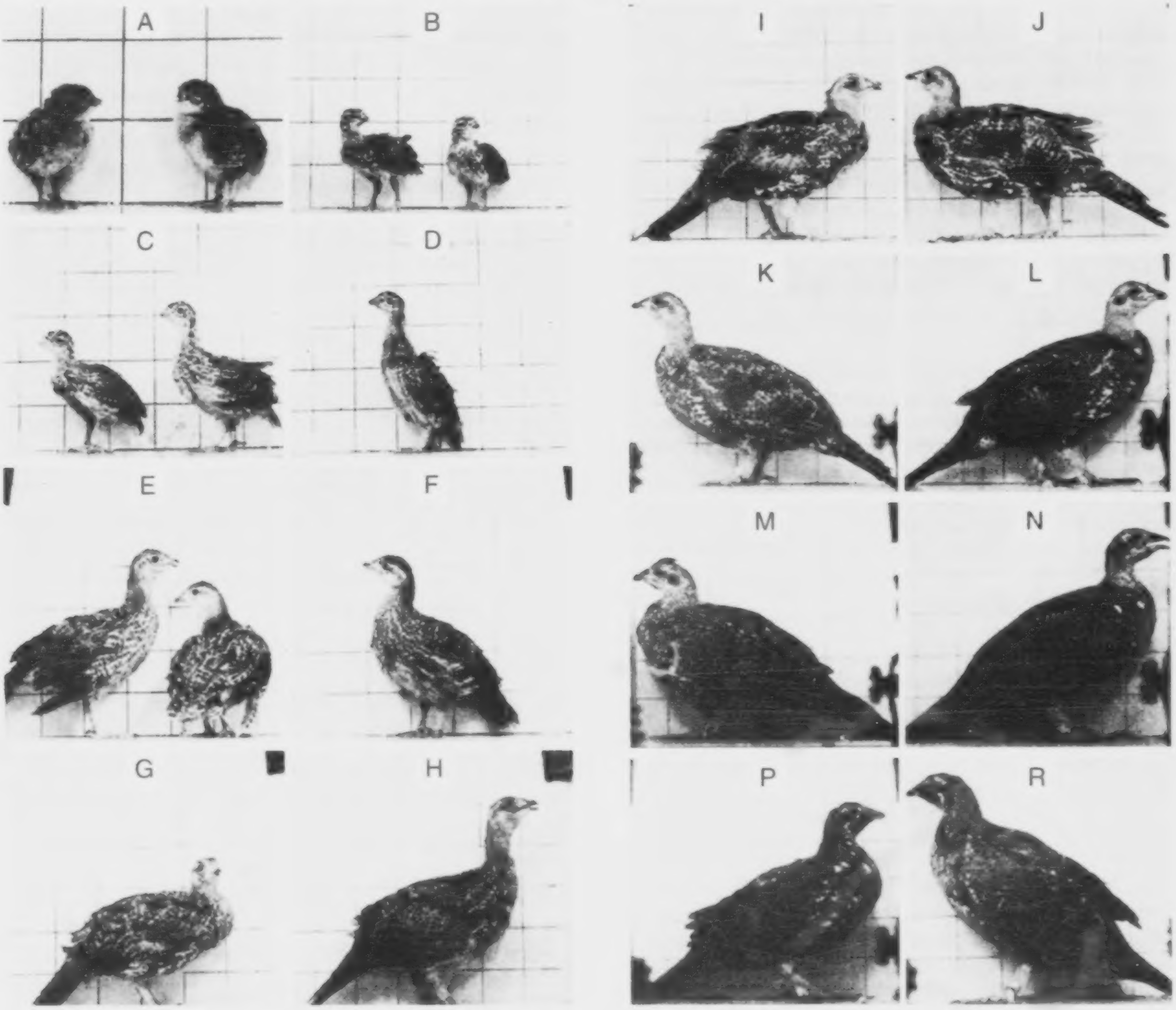
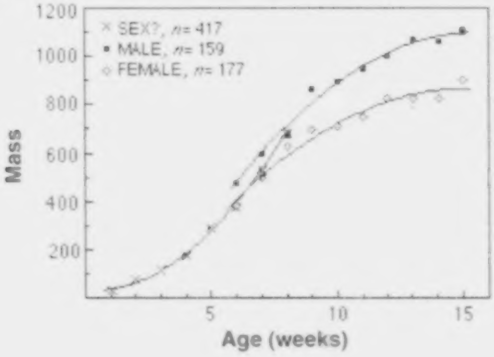


Fig. 11.6. Mean weekly body mass (g) of juveniles 1–15 weeks of age, westcentral Montana. Data from Table 4 of Schladweiler (1974).



11.2 Growth of feet, wings, principal breast muscles, and selected internal organs

11.2.1 Length of foot[8,9]

The feet of males and females from Comox Burn appear to grow at about the same rate (Fig. 11.7) [15a]. Both reached asymptotes at ~10 weeks of age, males at a mean length of ~99 mm and females at ~91 mm. These are the approximate lengths of feet of yearling males and females, respectively (Table 9.4). Thus, by 10 weeks of age, the foot is nearly full grown in both sexes. Clearly, the foot attains near maximum size while body mass is still increasing [15b]. At equivalent body masses in older juveniles, the foot of males was larger than in females, indicating that females have smaller feet than males relative to body mass.

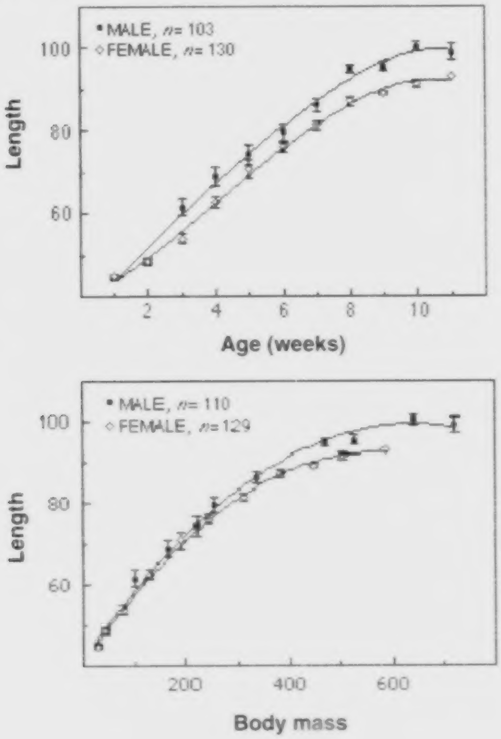


Fig. 11.7. Mean length of foot (mm ± SE) of juveniles regressed on age in weeks, and relationship between its length and body mass (g). Comox Burn, 1969–1978.

11.2.2 Length of wing[9,10]

Wings grow more slowly than feet, not beginning to reach an asymptote until ~13 weeks of age in both sexes (Fig. 11.8) [16a]. At this time, the wing has not attained the length of that of yearlings in either sex (male, 95% of yearling length; female, 94% of yearling length). Nevertheless, in early growth, the wing increases more rapidly than body mass [16b]. In contrast to the foot, wing length of females is the same as that of males at equivalent mass.

11.2.3 Major breast muscles

The two major breast muscles, *pectoralis major* and *pectoralis minor*, account for at least 25% of adult body mass (Table 9.4) in both sexes. At 1 and 2 days of age, they account for only 2% of body mass (*pectoralis major*, mean = 0.43 ± 0.04 g; *pectoralis minor*, mean = 0.13 ± 0.02 g; both *n* values = 16). They grow slowly for about the first week of life, then increase rapidly (Fig. 11.9) [17a, b]. By 10 weeks they account for ~20% of body mass, less than in yearlings and adults (see 9.2.1 and 9.2.2), but some 10 times greater than at 1–2 days of age. Rapid growth from 2 to 10 weeks coincides with rapid development of flight. It must also contribute to the development of thermoregulation, by providing an increasing proportion of thermogenic tissue relative to body mass (Ricklefs 1983). Both muscles increase mass linearly relative to that of the body (Fig. 11.10) [18a, b] and comprise a principal proportion of body mass by 4–5 weeks of age.

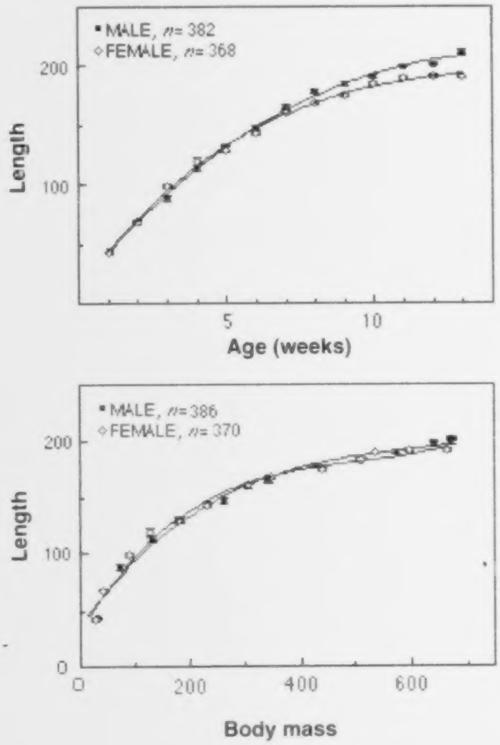


Fig. 11.8. Mean length of wing (mm ± SE) of juveniles regressed on age in weeks, and relationship between its length and body mass (g). Hardwicke Island, 1979–1984.

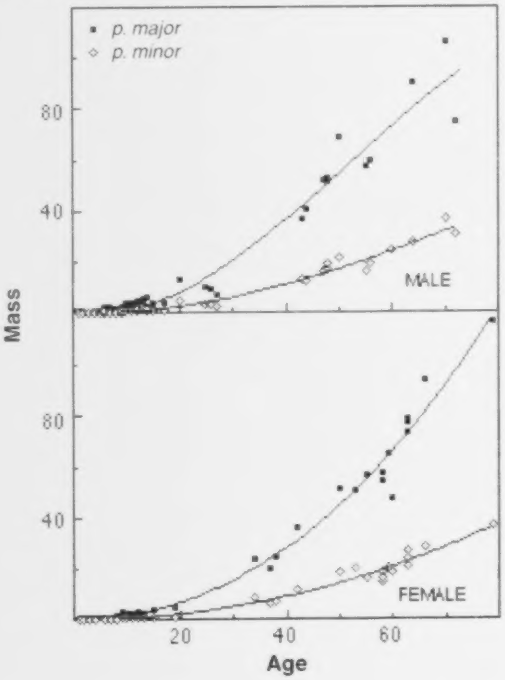
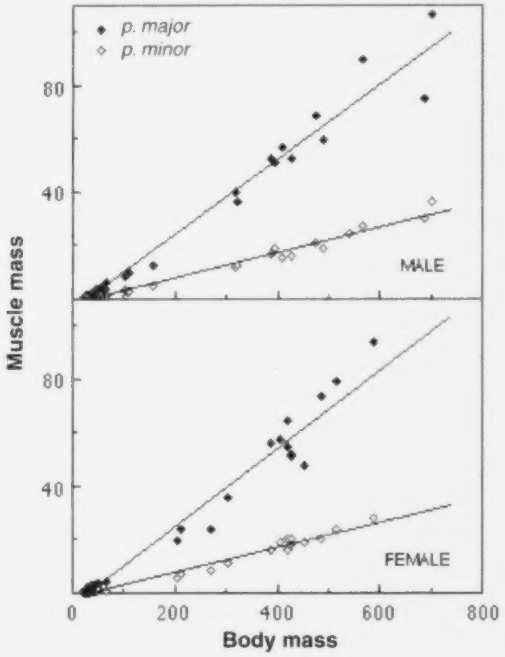


Fig. 11.9. *Pectoralis major* and *minor* muscle masses (g) of juveniles regressed on age in days. Data from Vancouver and Hardwicke islands combined.

Fig. 11.10. Relationship between *pectoralis major* and *minor* muscle mass (g) and body mass of juveniles. Data from Vancouver and Hardwicke islands combined.



11.2.4 Heart and liver

(a) *Heart.* Mass of the heart increases slowly for about the first 10 days of life (Fig. 11.11) [19a]. Those of males and females are similar to about 30–40 days of age but then begin to diverge; at about the same time body mass begins to diverge (Fig. 11.2). Mass increases linearly with that of the body [19b].

(b) *Liver.* As with the heart, the liver grows slowly for the first 10–15 days of life (Fig. 11.12) [20a]. Those of males and females have similar masses to ~30–40 days of age and then begin to diverge. They, too, increase linearly with body mass [20b].

11.2.5 Gastrointestinal tract

(a) *Gizzard.* The gizzard grows slowly up to ~30–40 days of age (Fig. 11.12) [21a]. At this time, those of the two sexes begin to diverge, as with the heart and liver. The gizzard increases linearly with body mass [21b].

(b) *Small intestine.* Length of the small intestine (the duodenum, jejunum, and ileum) increases rapidly in the first 30–40 days of life, then slows, and reaches an asymptote at ~70–80 days of age (Fig. 11.13 [22a]). Asymptotic length is approximately equal to mean lengths found in yearlings and adults (Tables 9.5–9.8). This organ clearly increases more rapidly than body mass in early life (Fig. 11.13) [22b], attaining mature length at a relatively young age.

Fig. 11.11. Heart muscle mass (g) of juveniles regressed on age in days, and relationship between its mass and body mass. Data from Vancouver and Hardwicke islands combined.

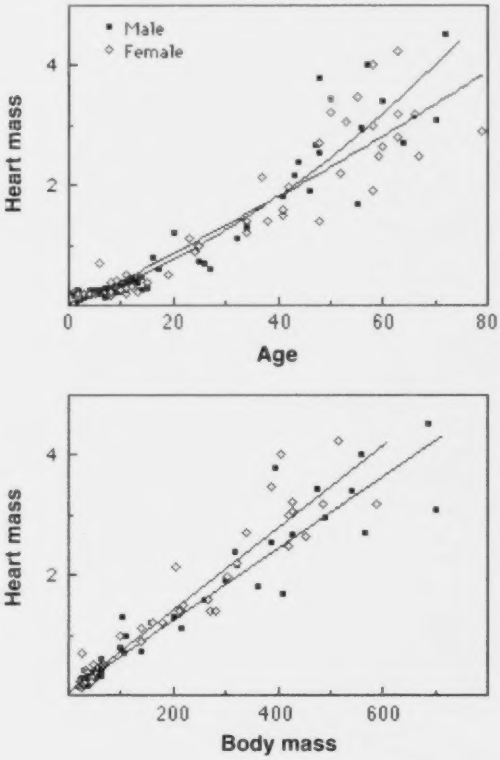


Fig. 11.12. Liver and gizzard masses (g) of juveniles regressed on age in days. Data from Vancouver and Hardwicke islands combined.

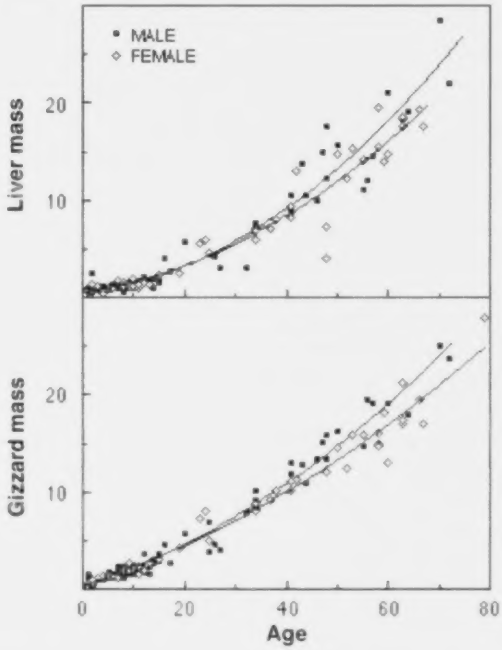


Fig. 11.13. Length of small intestine (cm) of juveniles regressed on age in days and relationship between its length and body mass (g). Data from Vancouver and Hardwicke islands combined.

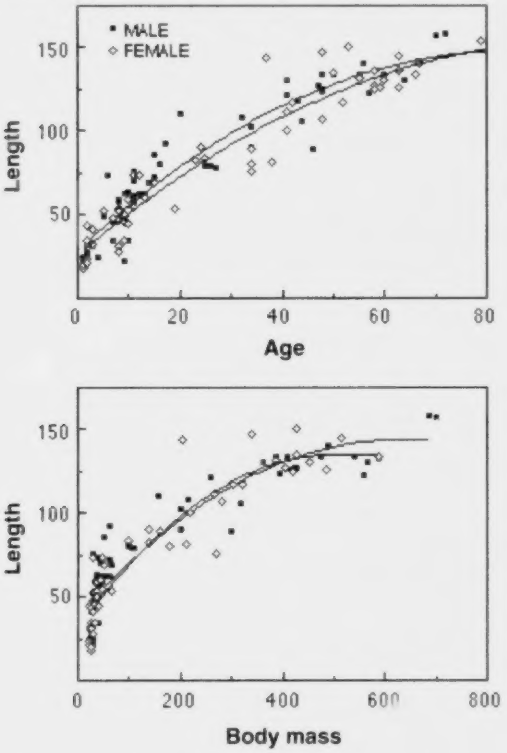
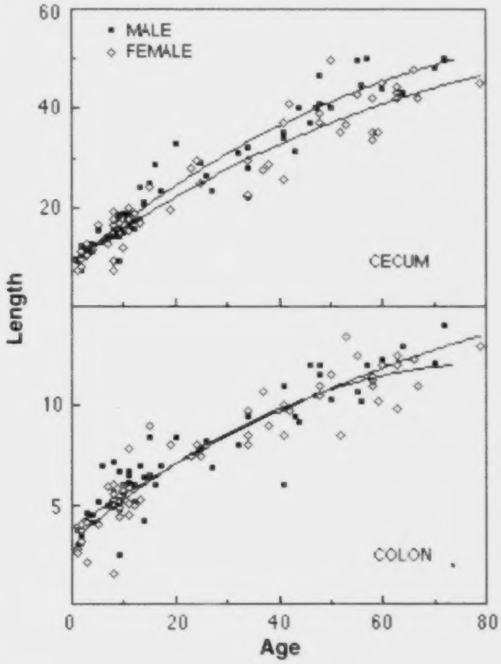


Fig. 11.14. Cecum (one only) and colon lengths (cm) of juveniles regressed on age in days. Data from Vancouver and Hardwicke islands combined.



(c) *Ceca.* Cecal length follows the same general pattern as the small intestine, but not increasing quite as fast in early life (Fig. 11.14) [23a]. At 80 days of age, lengths of the ceca are nearly equal to those of yearlings and adults (Tables 9.5– 9.8). This organ, too, reaches its asymptote at an early age [23b].

(d) *Colon.* The colon, the large intestine, has a growth pattern similar to that of the small intestine and ceca (Fig. 11.14) [24a]. At 80 days of age its length is nearly equal to that of yearlings and adults (Tables 9.5– 9.8). As with the small intestine and ceca, length of the large intestine levels off at an early age [24b].

Rapid development of most sections of the gastrointestinal tract facilitates digestion and appears to be adaptive for rapidly growing chicks. Slower growth of the gizzard may relate to the relatively soft foods taken by young birds in their first summer (see 12.1.2(c)).

(e) *The bursa of Fabricius.* A number of workers have examined the bursa of Fabricius of blue grouse, mainly with respect to its utility for determining age or breeding status. This small blind pouch is present in newly hatched chicks, opens into the cloaca, and regresses and disappears with age. Buss and Schottelius (1954) measured bursal depths of 23 *D.o. pallidus* in autumn and concluded (p. 137) that some grouse retain it "... until about two years of age when they apparently begin to breed." Bendell (1955*b*) examined bursae of 37 *D.o. fuliginosus* in summer at Lower Quinsam. He found that males and females may retain bursae into their second or third year. Based on breeding status of some of these birds, he concluded that presence of a bursa did not necessarily indicate a bird had not bred.

Caswell (1954*b*) measured this organ in *D.o. pallidus* in Idaho, on both breeding range and in autumn. He found an overlap in depths between juveniles and adults on breeding range and concluded that depth in autumn is not an infallible indicator of age. Standing (1960), working with *D.o. pallidus* on breeding range in northcentral Washington, recorded overlaps in depths of yearling and adult bursae.

We measured bursae of 146 blue grouse examined on various breeding ranges (Table 11.3). Modal depths of adult, yearling, and juvenile bursae were clearly separate, but as suggested by studies reviewed above, there was overlap by yearlings with both adults and juveniles. Data from birds shot by hunters and examined at the Chumstick Checking Station ($n = 387$) were consistent with data from breeding range.

On average, bursae of yearlings are intermediate in size between those of adults and juveniles, with most yearlings retaining it into their second summer. We agree with Bendell (1955*c*) and Standing (1960) that retention of a measurable bursa does not preclude breeding, for among seven yearling females with brood and for which we measured bursae, three had none and the others ranged from 0.2 to 1.2 cm in depth.

We conclude that up to about 1 October, bursae of adults of both sexes are usually ≤1.0 cm in depth, those of midsummer and early autumn juveniles, usually >1.0 cm in depth (very small juveniles may have bursae ≤1.0 cm, consistent with their body size, but this has not been documented). Those of yearlings confuse the picture, for their bursae may overlap with those of adults and juveniles, reducing the reliability of bursal depth for determining age.

Table 11.3. Bursal depths (by 0.5 cm categories) of adults, yearlings, and juveniles on breeding range[a] and among birds killed by hunters and examined at the Chumstick Checking Station, 1954–1959.[b] Modes are bold-faced.

	No. of adults		No. of yearlings		No. of juveniles	
Bursal depth	Male	Female	Male	Female	Male	Female
BREEDING RANGE						
0.0–0.5	**34**	**23**	3	**11**		
0.6–1.0	2	1	**17**	**11**		
1.1–1.5		8	4	1	1	
1.6–2.0		5	3	8	**11**	
2.1–2.5		1	1	1		
CHUMSTICK CHECKING STATION						
0.0–0.5	**43**	**23**		2	1	
0.6–1.0	7	8	**5**	3	1	2
1.1–1.5		2	2	**5**	5	14
1.6–2.0		1	1	2	**84**	**70**
2.1–2.5		1	1		33	48
2.6–3.0					13	9
3.1						1

[a] Includes birds from various study areas throughout much of the range of blue grouse; all but four were examined prior to 1 September. To minimize observer bias, only birds whose bursae were measured by FC Zwickel are included.

[b] Virtually all bursae were measured by FC Zwickel.

11.3 Plumage

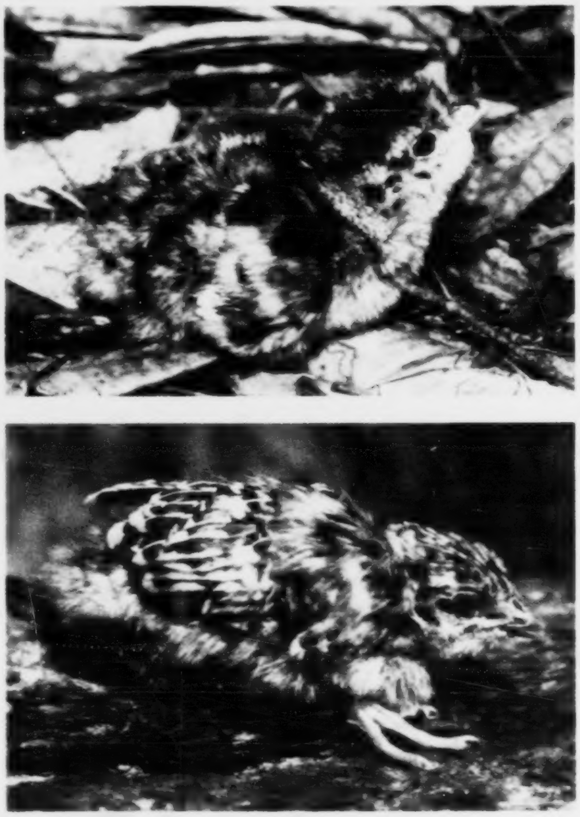
No one has conducted comprehensive studies of overall plumage development in juveniles. Bent (1932), however, provided a general and cursory review for *D.o. fuliginosus*, and Bendell (1955*b*) provided a more detailed description for this subspecies. Others have described the development of certain feather tracts, especially those of the remiges and rectrices as they relate to age (e.g., Van Rossem 1925; Smith and Buss 1963; Schladweiler 1974). We provide a general view of plumage development and follow this with a more detailed examination of remiges and rectrices.

11.3.1 General development

Newly hatched chicks are covered with down, the natal plumage. The first seven juvenal primaries are present at hatch, as at least pinfeathers. Some contour feathers are apparent within the first week of life (Fig. 11.15). By 2 weeks of age, contour feathers appear on sides of the chest and juvenal rectrices on the tail (Bendell 1955*b*). Bendell continues (p. 354), at 4 weeks, "... juvenal contour feathers sheath the top of the head, body, legs, and wings. The sides and back of the head and upper neck are still in natal down. ... the bird, except for the head [and belly], is in full juvenal plumage." Bent (1932) reported that the last natal down is on the belly and head. We found the last down, on the chin, to disappear at ~6 weeks of age at Comox Burn.

At 8 weeks, juvenal contour feathers on the shoulders and sides of the chest are being replaced by postjuvenal counterparts. The juvenal plumage is completed at ~10 weeks at Comox Burn. By 14 weeks, all postjuvenal contour feathers are nearly fully grown (Bendell 1955*b*). Thus, in the first summer, natal down is replaced by juvenal feathers, which are almost immediately replaced by postjuvenal feathers. Individ-

Fig. 11.15. Day-old chick (*top*), a ball of down. Note egg-tooth and tips of juvenal primaries of right wing emerging beyond the down. Photo by MA Degner. Compare to 6–7-day-old chick (*bottom*) with juvenal primaries at or near flight stage. Photo by J Kristensen.



uals may be clothed with various portions of 2–3 of these plumages at any particular time (see Fig. 8.1). Rapid development of juvenal plumage, in parallel with an increase in the ratio of pectoralis muscle to body mass, is closely associated with attainment of homeothermy and flight.

Smith and Buss (1963, p. 576–577) give more detail with respect to the development of selected feather tracts in aviary birds—summarized by us [data on primary growth in brackets are ours, extrapolated from Zwickel and Lance (1966) and Redfield and Zwickel (1976)]:

Week 1. Generally covered with down; juvenal feathers appearing in humeral tract; coverts for primaries 1 through 7 emerged [juvenal P1 completes growth about day 7].

Week 2. Juvenal P1 completed. Juvenal feathers emerge in lower cervical region of spinal tract and in femoral tract [juvenal P5 completes growth about day 14].

Week 3. Juvenal feathers spreading in spinal, humeral, femoral, and ventral tracts; down still present on leading edge of alar tract [postjuvenal P1 begins to grow about day 16].

Week 4. Juvenal feathers emerge in capital tract; heavy development of juvenal feathers in spinal and humeral tracts; light development on inner side of crural tracts [postjuvenal P2 begins to grow about day 22; P3 about day 26].

Week 5. Emergence of postjuvenal rectrices; growth of juvenal feathers nearly complete in alar tract [postjuvenal P3 is ~1/4 grown on day 35].

Week 6. Development of juvenal feathers in capital and crural tracts virtually complete; postjuvenal feathers appear in alar tract [postjuvenal P4 begins to grow about day 36; P1 completes growth about day 41].

Week 7. Growth of juvenal feathers in median cervical region of spinal tract complete [postjuvenal P5 begins to grow about day 43; P6 at about day 49; P2 completes growth about day 48].

Week 8. Growth of juvenal feathers in caudal tract complete. Postjuvenal feathers appear in capital tract [postjuvenal P6 is ~1/4 grown on day 55; P3 completes growth about day 55].

Week 9. Development of postjuvenal coverts in caudal tract [postjuvenal P7 begins to grow about day 61].

Week 10. [postjuvenal P7 is ~1/4 grown on day 68; P4 completes growth about day 64]

Week 11. Postjuvenal feathers emerge in auditory region of males [postjuvenal P8 begins to grow about day 75; P5 completes growth about day 74].

Week 12. Postjuvenal feathers in auditory region of males well defined [postjuvenal P8 is ~1/4 grown on day 84].

Week 13. Postjuvenal feathers in auditory region of males enlarging [postjuvenal P8 is ~1/4 grown on day 90; P6 completes growth about day 87].

Week 14. Postjuvenal feathers in auditory region of males enlarging and beginning to merge with capital tract [postjuvenal P8 is ~2/3 grown on day 97].

Week 15. Postjuvenal feathers cover head and neck [postjuvenal P8 is ~3/4 grown on day 100; P7 completes growth about day 104].

Week 16. Development terminated in capital tract; terminating in all other tracts [postjuvenal P8 still ~3/4 grown on day 100].

Week 17. [postjuvenal P8 is ~7/8 grown on day 107]

Week 18. [all postjuvenal primaries fully grown about day 123]

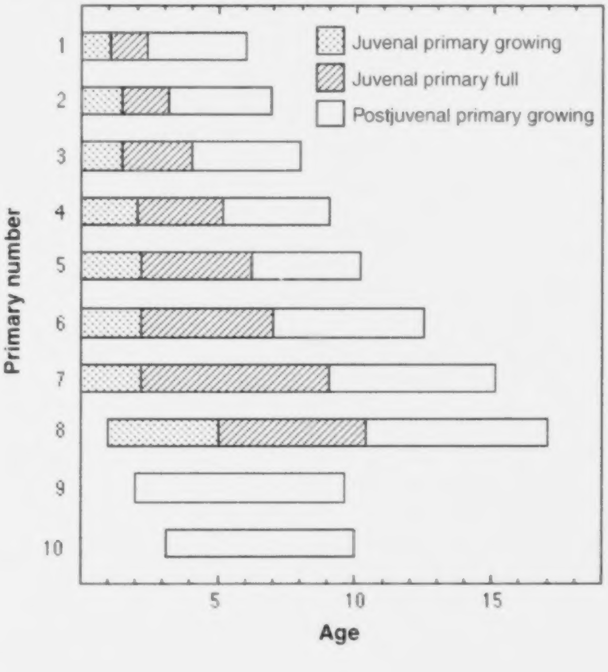
Aviary birds may not represent exact timing of changes in wild birds. Nevertheless, in conjunction with photos (Fig. 11.5), they illustrate the rapid changes in plumage with age and are consistent with our more general observations of wild birds. Schladweiler's (1974) photos of aviary birds from hatch to completion of the postjuvenal plumage are similar to those of Smith and Buss.

11.3.2 The remiges

(a) *Primary remiges.* The first juvenal feathers to appear are the primary remiges, the primaries (Ps). Newly hatched chicks have seven that range from unopened pinfeathers to those with vanes up to 11 mm in length.[11] The approximate progression of growth of Ps 1–7 during the first 15 days of life can be seen in Fig. 2 of Zwickel and Lance (1966). Primary 8 first appears in the second week of life (Schladweiler 1974), and Ps 9 and 10 in weeks 3 and 4, respectively (Smith and Buss 1963[12]; Schladweiler 1974).

Juvenal primaries grow rapidly, providing chicks with flight ability at an early age (14.3.3(e)). At ~16–17 days of age, P1 is shed, initiating growth of the first postjuvenal replacement (Fig. 11.16). Postjuvenal primaries also grow rapidly, presumably an adaptation for maintaining, and develop-

Fig. 11.16. Approximate timing of primary development in juveniles, by age in weeks. Composite depiction derived from Smith and Buss (1963), Zwickel and Lance (1966), Schladweiler (1974), Redfield and Zwickel (1976), and unpublished data.



ing, flight ability. By ~17 weeks of age, all postjuvenal primaries are fully grown. Termination of growth of P8 signals the end of development of the postjuvenal (Basic 1), or first-winter, plumage, which generally resembles that of adults (8.1.2).

Primaries 9 and 10 deserve special note, for they appear later than the others (Fig. 11.16) and are of a shape and colour somewhat different than Ps 1–8 (see 8.1.2).[13] They are not moulted until the bird's second autumn.

(b) *Secondary remiges*. Less attention has been paid to development of secondary remiges, the secondaries (Ss). Bendell (1955*b*) noted that at least 12 juvenal secondaries are actively growing in each wing by 2 weeks of age and suggested their moult is irregular.

Smith and Buss (1963) provided the greatest detail on development of the secondaries, as based on four aviary chicks. These birds, all from one brood, first shed juvenal S3 (counting distal to proximal) at 5 weeks of age. (Bendell 1955*b* indicated the secondary moult began at 6 weeks in wild birds.) Shedding proceeded in numerical order to S9, at 9 weeks, at which time S2 also was lost. S12 was shed at 10–11 weeks, and S1 (the last to drop) at 11–12 weeks. With only slight variation, this pattern was adhered to by all four birds. Except for S1 and S2, the moult described for this brood was consistent with Bendell's (1955*b*) observation that it proceeds mediad from the wrist. At 14 weeks, Bendell (p. 355) found all postjuvenal secondaries ". . . approximately fully grown".

We examined secondary development of a few wild chicks at Comox Burn. Juvenal S3 was first to be lost, at ~5 weeks of age. All juvenal secondaries were fully grown at ~7 weeks, by which time S4 and S5 were shed. This is in close agreement with the findings of Smith and Buss, above.

11.3.3 The rectrices

Juvenal rectrices first appear in the second week of life (Bendell 1955*b*; Smith and Buss 1963). Bendell says they are approximately one-half grown at 4 weeks of age. Their moult begins with the outer pair and proceeds in order from each side toward the centre (Van Rossem 1925; Smith and Buss 1963). Van Rossem says juvenal rectrices are shed by 2–3 weeks of age, but Smith and Buss found birds in their aviary to first shed tail feathers at 5 weeks, and Bendell, working with wild birds, at 6 weeks. In the aviary, 1–4 feathers had been dropped at 5 weeks. (Smith and Buss 1963). By 9 weeks in our aviary birds, and by 10 weeks in wild birds at Comox Burn, all juvenal rectrices were lost.

The first postjuvenal rectrices emerge at 5 (Smith and Buss 1963) to 6 weeks (at Lower Quinsam; Bendell 1955*b*), and at 5–6 weeks in wild birds at Comox Burn. Bendell says they are approximately one-half grown at 8 weeks at which time they extend beyond the juvenal rectrices still present. Growth of postjuvenal rectrices is completed by ~14 (Bendell 1955*b*) to 16 (Smith and Buss 1963) weeks of age.

The young grouse is never completely covered in only juvenal plumage (Fig. 8.1), for throughout much of its development natal down fills some feather tracts, and by 16–17 days of age, juvenal primaries are being replaced by postjuvenal feathers. In the first 2 weeks of life the plumage is a mixture of down and juvenal feathers; from the third to seventh or eighth week, a mixture of down, juvenal, and postjuvenal feathers; and from ~8 to 14 weeks, a mixture of juvenal and postjuvenal feathers. Full postjuvenal plumage, attained at ~14 weeks and completed at ~17 weeks, is carried through the first winter and into spring when these birds are now classified as yearlings.

11.3.4 Determination of sex by plumage

The earliest criterion for identifying sex of juveniles by plumage appears at ~6 weeks of age, with development of the postjuvenal upper tail coverts (McFetridge 1972; Nietfeld and Zwickel 1983). Postjuvenal upper tail coverts of males are black or blackish, with gray flecking and narrow whitish gray bars, while those of females are black to blackish brown with bold light brown bars, the shade varying among individuals and subspecies. White feathers surrounding the lateral cervical apteria of males first appear in the postjuvenal plumage and can be used as a sex distinguishing character from ~8 weeks of age (Caswell 1954*a*); those of females are gray, as in adults.

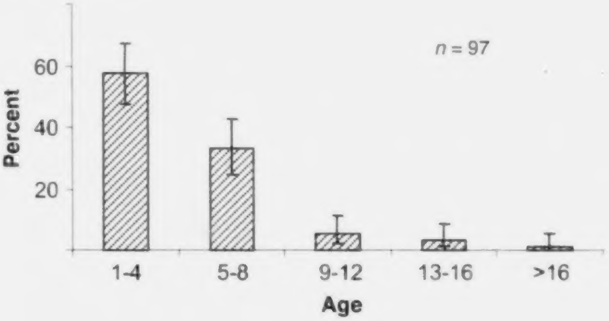
11.4 Homeothermy

In general, birds hatch with only partially developed thermoregulation (Welty and Baptista 1988). There are no specific studies of the development of homeothermy in blue grouse, nor in most North American grouse. Nevertheless, young galliforms use brooding beneath a parent as a form of behavioural thermoregulation (Myhre et al. 1975; Pedersen and Steen 1979), and one can gain some insight into this question by examining ages at which chicks are brooded.

At Comox Burn and Hardwicke Island, we found 97 hens brooding young and for which we knew approximate ages of the chicks (Fig. 11.17). Among these broods, 58% were composed of chicks ≤4 days of age. Over 90% were ≤8 days of age. Thus, homeothermy appears quite well developed in blue grouse by 8 days of age, as in willow ptarmigan (Myhre et al. 1975; Boggs et al. 1977). Only one chick >16 days of age, estimated at 25 days, was being brooded. Clearly, most chicks can thermoregulate by ~16 days of age, at least at ambient temperatures occurring at Comox Burn in daylight hours.[14]

Circumstantial evidence, clocker-like droppings (12.5.3) of brood hens with very small chicks (Zwickel 1967*a*), suggests they are brooded throughout the night. Those >8 days of

Fig. 11.17. Frequency distribution of chicks (%) brooded by hens by 4-day age classes. Data from Comox Burn and Hardwicke Island combined.



age may be brooded more at night than indicated by data above, for in field aviaries they use artificial brooders up to ~3 weeks of age.

11.5 Synthesis

Young blue grouse grow rapidly, with some structures and organs maturing sooner than others. Growth is allometric.

As with egg mass (see 10.4.2), body mass at hatch varies among populations. Males are approximately the same mass as females on day 1 but by 3–4 weeks of age are clearly heavier and continue to diverge to at least 13 weeks of age. Available information indicates that interior chicks are smaller on day 1 than coastal chicks, but that they have a faster rate of growth. More rapid growth may relate to different nutritional regimens in the markedly different habitats used by the two subspecies groups, or may be an adaptation to cope with earlier and more severe winter conditions than in coastal areas.

Some structures and organs mature at an early age, e.g., the foot, wing, and intestinal tract. Growth of these structures soon slows, to reach asymptotic lengths, at ~10–13 weeks of age, that are equivalent to those in yearlings and adults. Early maturity of the foot, wing, and breast muscles is clearly related to a need for early mobility, and that of the gut tract is almost certainly an adaptation to a rapidly changing food and nutritional regimen in the first summer of life. All organs do not follow this pattern. For example, the heart, liver, and gizzard grow more slowly and generally parallel changes in body mass.

Plumage development, too, is very rapid, providing flight capability by the end of the first week after hatch and completion of the postjuvenal plumage by ~17 weeks of age. Rapid growth and turnover of flight feathers is accompanied by rapid growth of the major breast muscles. These changes are adaptive for a ground-nesting species that is precocial and flightless at hatch, and growing very rapidly.

Coincident with morphological changes, very young chicks also increase thermoregulatory abilities. Evidence from ages at which chicks are brooded suggests reasonably well-developed homeothermy by 8 days of age. Ages at which chicks are brooded also may vary with weather, for there is evidence that lengths of brooding bouts vary with meteorological conditions. Brooding ages may differ among populations, as related to local climate, but this is speculative, for there are no data on this point. Growth and development are clearly complex and dynamic processes, for which we have only a rudimentary knowledge in blue grouse.

Endnotes [Chapter 11]

1. Body mass and plumage development are the only growth parameters of blue grouse reported by others so examination of other parameters is limited to our studies in coastal British Columbia. Foot measurements are from birds at Comox Burn. We first measured wings at Hardwicke Island and used these data to examine this parameter. Internal body measurements are from birds collected at Comox Burn and Hardwicke Island. Most were taken in removal studies at Comox Burn (Zwickel 1972*a*, 1980), but a few are from birds that died during handling or were collected for other studies.

2. Our largest sample of body mass for young grouse is from banding studies and birds killed by hunters from Comox Burn and vicinity. We use these data for these analyses.

3. Percentage loss from hatch to day 3 was undoubtedly even greater because large amounts of yolk are used on day 1 (Marcstrom 1960), and no wild chicks were examined at exact time of hatch. Two newly hatched chicks from wild eggs in our aviary had yolk and yolk sacs of 6.3 and 7.4 g, respectively.

4. Chicks without detectable yolk sacs were first found at 6 days of age (2/6 with none); 9/11 at 9 days of age had none; and none was found in chicks >9 days of age.

5. Dry mass of residual yolk equals about one-half the dry mass of newly hatched capercaillie and in the first 2.5 days of life accounts for most of the chick's energy requirements. By 2.5 days of age, three-quarters of the yolk present at hatch has been utilized, and the chick is largely dependent on outside sources of energy. Residual yolk is an important source of energy in the first days of life.

6. The latter analysis combines birds of all ages and does not take into account that rate of gain changes with age (Fig.11.4).

7. We identified sex of some birds in the younger age groups and analysed our data for all ages by sex.

8. One foot of each bird was measured from back of the bent heel (juncture of the tibiotarsus and tarsometatarsus) to end of the middle toe, excluding the claw.

9. Lengths of the foot and wing should be less subject to short-term seasonal or environmental influences than body mass. Combined with mass, they may be used to provide at least a crude index of condition. We leave an examination of condition to a future publication.

10. One wing of each bird was measured from the bent wrist (juncture of the radius–ulna and proximal carpals) to end of the longest primary, with primaries flattened.

11. This range is based on feathers of chicks measured at the nest, which may include birds up to a full day of age (McKinnon and Zwickel 1988). Vanes of most chicks measured at the nest were less than 5 mm long, and it is likely most primaries at hatch are in the pinfeather stage, for we measured chicks only after they had dried, many toward the end of their first day.

12. Smith and Buss counted primaries from distal to proximal, but most workers count proximal to distal, the order in which they develop and are moulted. We changed the numbering of Smith and Buss to read from proximal to distal.

13. Van Rossem considered P9 and P10 of young birds as postjuvenal feathers but Bendell (1955*b*) and Braun (1971) considered them as retained juvenal feathers. Arguments can be made to support either stand. We follow Van Rossem.

14. Rapid growth necessitates early development of thermoregulation, for a brood would soon exceed the ability of hens to cover them.

CHAPTER 12

Food, Nutrition, Water, Grit, and Excretion

While there are certain animal species which are entirely carnivorous, the plant kingdom is the original and essential source of all animal life, . . .

LA Maynard and JK Loosli (1962)

Food and water supply basic needs for reproduction, growth, and maintenance. Both are proximally important to the individual and populations in limiting distribution and abundance and, ultimately, in contributing to evolution of the species. In some birds, including blue grouse, that forage on hard or fibrous foods, grit is used for mastication, and, perhaps, as a source of minerals. Fecal excreta (droppings) mainly represent undigested portions of the diet. We consider these topics separately, but all are interrelated.

12.1 Food

Blue grouse are primarily vegetarians throughout the year. Principal exceptions include young chicks, which feed heavily on invertebrates in the first days or weeks of life, and older chicks and females that may take large numbers of insects if available, especially grasshoppers (Arididae and Locustidae), in mid to late summer.

Food habits of this grouse differ markedly between winter and spring, summer and autumn. Along with spruce grouse, sharp-winged grouse, and capercaillie, the winter diet is comprised mainly of needles, buds, and twigs of conifer trees. In this respect, they are virtually monophagous in winter, although species used may vary. This ability to thrive on a nearly monophagous diet of conifers is restricted to a small number of vertebrates, and few birds. The spring, summer, and autumn diet is much more varied and includes leaves, twigs, flowers, and fruits of various herbs, deciduous trees, and shrubs, with, in some areas, a considerable component of coniferous vegetation. In these seasons, the diet often varies among sex and age classes of birds.

Blue grouse have a well-developed crop in which they can store 45 g (Beer 1943) or more of food during feeding bouts.[1] Small stones, "grit", or hard seeds (Beer and Tidyman 1942), are used for grinding food within their muscular gizzard (ventriculus).

12.1.1 Feeding behaviour

Blue grouse feed to a greater or lesser extent throughout the day, interspersed between other activities such as singing (in males), resting, preening, etc. Intense feeding occurs at dawn and dusk (King 1968), prior to roosting for the night.[2] King found most birds had only partially filled crops in midday.

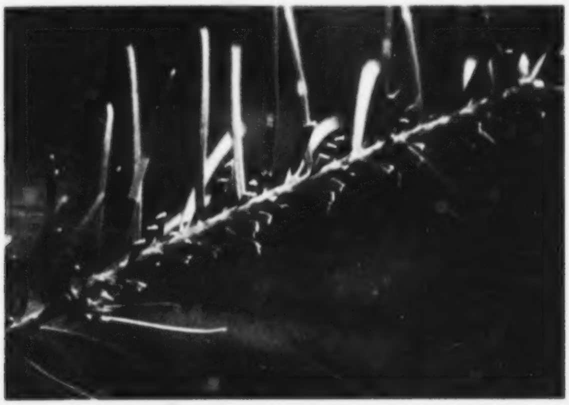
This grouse feeds by pecking at and securing objects in its beak. Individual items, e.g., insects, may be captured by a quick peck and swallowed whole. Attached items such as buds, flowers, leaves, and berries are held in the beak and separated from the rest of the plant by a pulling and (or) shearing motion, a quick and slightly sideways tilt of the head. Buds and needles may be taken alone or with small portions of twigs. Grouse can cleanly shear off 75% or more of a 2–3 cm long conifer needle, leaving the base attached to the twig (Fig. 12.1). They often take many needles from a single plant during a feeding bout. They do not use their feet to find (scratch for) or secure food (except that they may jump up for items slightly out of reach).

(a) *Winter*. In this season, blue grouse spend most of their time in conifer trees, their principal source of food. They may roost at night in species little used for feeding, e.g., subalpine fir, and move to more preferred species to feed (Pekins 1988). Or they may roost and feed in the same tree if a preferred food species provides adequate roosting cover. Remington (1990) found little use of subalpine fir for roosting in stands dominated by Douglas-fir but heavy use in those dominated by lodgepole pine [used for feeding but presumably a less protective roost site]. Needles, buds, twigs, staminate and immature pistillate cones (mainly in spring), and occasionally seeds (mainly in autumn), may be eaten. Birds presumably feed sporadically throughout the day in winter, probably most heavily in crepuscular periods. In areas with short day lengths, they likely fill their crops in crepuscular hours.

(b) *Spring and summer*. On breeding range, most feeding is from the ground but birds may fly into trees or shrubs for newly emerging leaves prior to widespread availability of herbs (but see territorial males, below). They may seek new plant growth as it becomes available, e.g., leaves or flowers of emerging herbs, deciduous trees, or shrubs; swelling buds, young cones and needles of conifers, and, when ripe, various fruits.

Territorial males feed almost exclusively within the confines of their territories. In coastal areas, where they are primarily arboreal, they tend to feed within trees from which they sing, although those with territories on early forest seres after

Fig. 12.1. Douglas-fir needles clipped by grouse, Middle Quinsam.



clear-cut logging or fire feed mainly from the ground. At peak breeding season, males with territories spend much time singing but break for short feeding sessions between bouts of song. Females, especially in early spring, may move to clearings for foraging (Bendell and Elliott 1967). Those incubating eggs feed voraciously when off the nest.

Feeding habits change with the seasons. Hens with broods, especially, may seek open (Wing et al. 1944; Armleder 1980), mesic sites (Mussehl 1963*a*; Bendell and Elliott 1967) with lush vegetation; areas that provide an abundance of insects for young chicks (Beer 1943; Wing 1947). As fruits ripen, broods may concentrate in berry-producing areas, often flying into shrubs to forage. With the advance of summer, birds on xeric ranges tend to concentrate in mesic sites (Marshall 1946; Zwickel 1973) or those with greater canopy cover (Wing et al. 1944; Armleder 1980) as vegetation desiccates in open areas. This may relate to foraging and (or) microclimate (Zwickel 1992).

Newly hatched chicks are a special case. They peck at items, plant and animal, on their first day out of the nest. They move steadily and test items as they come upon them, without necessarily finishing a plant or cluster of insects. They peck at tips and undersides of leaves and occasionally at the ground.[3] They may run after insects or jump into the air to obtain them, or a berry or leaf from an overhead plant. Hens appear to determine travel routes but do not feed the young or seem to direct them to specific items. In contrast to some galliforms, hens do not scratch for food for the young. Once able, chicks often fly into taller shrubs to feed on berries, and gradually assume the feeding habits of older birds.

(c) *Autumn*. This is a period of transition when grouse are shifting to a winter diet. Many females and juveniles are migrating, passing through different plant communities and taking foods opportunistically. Grouse already on winter range, mainly yearling and adult males and unsuccessful or non-breeding females, are returning to a diet dominated by conifer needles.

12.1.2 Major types and taxa of foods and their selection

Owing to the broad range of habitats in which blue grouse are found, species of foods taken vary widely. Some species, or higher taxa, are heavily used, others avoided. Six studies of foods of this bird are most comprehensive: Beer (1943), Stewart (1944), Standing (1960), King (1973), Schladweiler (1975), and King and Bendell (1982).[4] We lean most heavily on results of these studies in describing food habits of this bird.

(a) *Winter*. Conifers were recognized as a principal food of blue grouse through much of the year as early as the 1850s (G Suckley, in Baird et al. 1874), but not until the study of Beer (1943) was there an attempt to quantify their use. Beer shows them as the principal food from September through April, providing nearly 100% of the diet from November through March (Figs. 12.2 and 12.3). Stewart (1944) also found conifers to be a principal component of the winter diet (±90%). They figured heavily in winter droppings collected in seven western states (Zwickel and Bendell 1986), contributing >90% to samples in most areas examined. They also were the major component in winter droppings from Hardwicke Island, contributing >95% of foods identified (Hines 1987), and in crop samples from grouse collected in subalpine Vancouver Island (Figs. 1 and 2 of King (1973)).

Beer (1943) found Douglas-fir to be most heavily used in interior, true firs (*Abies* spp.) in coastal, habitats in winter, with pines (*Pinus* spp.) less favoured. Stewart (1944) also

Fig. 12.2. Year-round classes of foods of adults by month. Redrawn from Beer (1943).

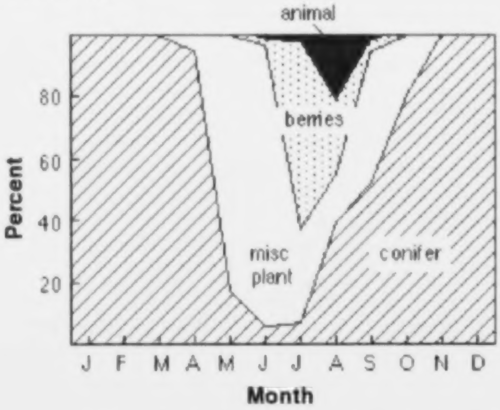
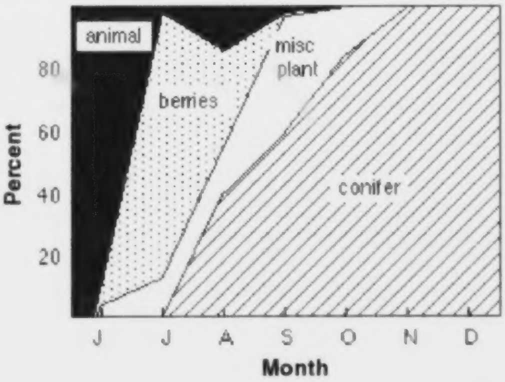


Fig. 12.3. Summer to midwinter classes of foods of juveniles by month. Redrawn from Beer (1943).



found heavy winter use of Douglas-fir by interior grouse (78% by volume), and of true firs by coastal birds (65%). Hemlock (*Tsuga* spp.), pine, and spruce (*Picea* spp.) were taken in lesser quantities. Small amounts of buds and twigs of wild cherry (*Prunus* sp.), willow, and aspen; twigs of dwarf mistletoe (*Arceuthobium* spp.); leaves of Anemone, alum-root (*Heuchera* sp.), small cranberry (*Vaccinium oxycoccas*), foam flower (*Tiarella trifoliata*), ferns, and mosses; and fruits of rose, manzanita (*Arctostaphylos* sp.), juniper, and salal were found. On the basis of a general correlation between the distribution of Douglas-fir and true firs with blue grouse, Beer (1943, p. 43) concluded, "The distribution of . . . [blue grouse] appears to be limited by that of the plant genera *Abies* and *Pseudotsuga*."

More recent studies indicate Douglas-fir and true firs do not dominate winter diets in some areas (Table 12.1). Douglas-fir is rare above 51°N in coastal British Columbia, and uncommon above ~53°N in interior British Columbia. It is not found above ~55°N in this region, but blue grouse range to ~63°N. Among these species, only subalpine and amabilis fir are common north of the range of Douglas-fir, and neither has been reported as an important winter food. Hines (1987) found western hemlock, and King (1973), mountain hemlock, to dominate winter diets on Hardwicke Island and in subalpine Vancouver Island, respectively. Belding (1892) and Swarth (1911) reported the use of western hemlock in California and southeast Alaska. Even Beer (1943) noted that western hemlock may be the primary winter food in some coastal areas. As well, blue grouse winter in some areas in which neither Douglas-fir nor true firs are found (Zwickel and Bendell 1986). Hence, the correlation between its distribution and that of Douglas-fir and true firs is only partial and unlikely to be a causal relationship.

Within genera, some species of plants may be used more than others. In Utah (Pekins 1988), Colorado (Remington 1990), and other southern areas (Zwickel and Bendell 1986), subalpine fir, though common, may be avoided as food. In the Sierra Nevada, white fir (Hoffmann 1961), and in coastal Washington, noble (*Abies procera*) and grand (*Abies grandis*) fir (Beer 1943), are primary foods. Different pines may be used selectively. Lodgepole pine provides most of the winter diet in some areas (Boag 1964; Remington 1990), limber pine in others (Zwickel and Bendell 1986; Remington 1990), with ponderosa and white pine (*Pinus monticola*) perhaps less preferred (Zwickel and Bendell 1986). Pinyon pine may be used by some Great Basin populations (Pekins et al. 1989).

Along with subalpine fir, other common conifers that appear little used as food are western red cedar (pers. observ.), yellow cedar (King 1973), juniper (Beer 1943), and, in most areas, spruce (Beer (1943) reported light use, Stewart (1944) fair use, of spruce). Where Douglas-fir and pines are both available, pine (likely lodgepole or limber pine) may be preferred (Zwickel and Bendell 1986). Zwickel and Bendell ranked preference among the major genera of conifers as *Pinus* > *Pseudotsuga* > *Tsuga* > *Abies* > *Picea* > *Juniperus*. Remington (1990) reported a generally similar ranking among *Pinus*, *Pseudotsuga*, *Abies*, and *Picea* except that he considered *Pseudotsuga* > *Pinus* and *Abies* = *Picea*.

The only non-conifer implicated as a possibly important winter food is mountain mahogany (*Cercocarpus ledifolius*), in parts of the Great Basin (M Wickersham, pers. comm., Zwickel and Bendell 1986; Pekins et al. 1989), where conifers (except pinyon–juniper) are sparse, but this is not well documented. As well, Rogers (1968) reported that some blue grouse winter on "brush range" up to 16 km from the nearest conifers in parts of Colorado. If true, other plants must be used in these areas. Trace amounts (<1%) of serviceberry, sage, saltbush (*Atriplex* sp.), and wild buckwheat (*Eriogonum* sp.) have been found in winter droppings of birds from Arizona, Nevada, and Utah (Zwickel and Bendell 1986). Animal matter has not been reported as winter food.

Table 12.1. Amount of conifer and principal genera in the winter diets of blue grouse.

Area	% conifer	Contributions of principal plant genera (%)
Interior[a]	95	78 *Pseudotsuga*
Coastal[a]	89	65 *Abies*
BC, lowland	95	57 *Tsuga*[b]
BC, subalpine[c]	96	75 *Tsuga*
Arizona[d]	89	81 *Pseudotsuga*
California[d]	98	84 *Abies*
Idaho[d]	100	69 *Pinus*
Montana[d]	98	49 *Pseudotsuga*; 49 *Pinus*
Washington[e]	98	84 *Pseudotsuga*

[a] From Stewart (1944), composite samples from interior and coastal subspecies, respectively. See Beer (1943) for similar results.

[b] From Hines (1987), samples from Hardwicke Island; mean for all sex–age classes combined: adult males ate mostly western hemlock (93%); adult females and juveniles, mainly Douglas-fir, 62% and 70–73%, respectively.

[c] From King (1973), samples from Vancouver Island.

[d] From Zwickel and Bendell (1986), composite samples from one or more sites within a state.

[e] From Standing (1960), March-only samples from northcentral Washington (*D.o. pallidus*).

In summary, Douglas-fir and pines, especially lodgepole and limber pine, are major winter forages where they occur. In their absence, several species of true firs (especially grand and noble fir (Beer 1943) and white fir (Hoffmann 1956)), mountain hemlock (King 1971), and western hemlock (Beer 1943; Hines 1987) may dominate the diet. Pelren (1997) found Douglas-fir and ponderosa pine about equally in 15 winter crops from northeastern Oregon.

(b) *Spring*. This is a period of transition as birds move into breeding habitats. A great variety of different herbs and leaves of deciduous shrubs and trees may be taken, those classified as miscellaneous plants by Beer (Figs. 12.2 and 12.3). Species used vary among areas.

The proportion of coniferous plants in the spring diet declines, more so on interior than coastal breeding ranges (Stewart 1944). In shrub-steppe areas, conifers virtually disappear from the diet. For example, Standing (1960), working with *D.o. pallidus*, found coniferous food to drop markedly between February and March (>98% conifer, frequency of occurrence = 14/15 samples; computed by us from data in Standing) and April (<1% conifer, frequency of occurrence = 4/31 samples). In coastal areas, conifers may dominate the diet of territorial males; e.g., 18 crop samples collected by us from tree-singing males in California, Oregon, and Washington were composed of 38% conifer needles, 55% staminate cones, and 6% immature pistillate cones, a total coniferous component of 99%. In Montana, coniferous material provided 82% and 9% of the contents of spring crops of adult males and females, respectively; broad-leaved herbs, 15% and 88% for each sex, respectively (Schladweiler 1975). Coastal females also eat more broad-leaved plants in spring than do males. On Vancouver Island clear-cuts, approximately twice as much broad-leaved material is taken by females as compared to males in May and early June (King and Bendell 1982).

Birds that remain in the subalpine in spring do not have the same diversity available to them because of heavy snow pack. In subalpine Vancouver Island, conifers dominated the spring diets of males and females (Figs. 1 and 2 of King 1973), with males taking more coniferous material than females (>90% and >50%, respectively), as in other areas for which sex-specific data are available (Schladweiler 1975; King and Bendell 1982).

Species composition and abundance of potential plant foods change rapidly in spring. New leaves are emerging, growth is rapid, many plants are flowering, and some annuals soon desiccate and die. Use of particular species varies in part with phenology, among and within plant communities.

Beer (1943) reported that 69 genera of plants were known to be eaten by blue grouse, 45 of which he identified. Because of the low number of genera or species used in winter, the greatest diversity clearly occurs in spring, summer, and autumn. He found willow leaves to be an important spring food and thought (p. 36), ". . . its new leaves perhaps being a welcome change from the diet of conifers".

Stewart (1944) considered diets of interior and coastal blue grouse separately. Interior birds consumed considerable quantities of Douglas-fir and small amounts of pine in spring. He found needles of pines (in southern regions), Douglas-fir (in central regions), and Sitka spruce (in northern regions) in the spring diets of coastal birds. Staminate cones of true firs and Douglas-fir were eaten in moderate quantities. Leaves of pussytoes (*Antennaria* sp.), wild buckwheat, and hawkweed were taken in appreciable quantities. Leaves of ferns and white clover (*Trifolium repens*), and buds and twigs of aspen, were taken in modest amounts by some birds.

On lowland Vancouver Island, Douglas-fir needles and willow leaves were primary foods in March and April, with females taking more willow and fewer needles than males (King and Bendell 1982). Males continued to take large amounts of Douglas-fir and small amounts of seven other species of plants in May and June.

Zwickel and Bendell (1972*b*) compared crop samples of incubating females on two areas of Vancouver Island that were in different stages of secondary succession. At Comox Burn, 8–9 months after wildfire, leaves and buds of salal, willow, and bracken fern were principal foods (each contributing 20%–22% by volume), with Douglas-fir, western hemlock, and hairy cat's ear each contributing 6%–9%. Twenty-one species of plants were recorded, most providing less than 1% of the diet. At Middle Quinsam, ≥10 years after wildfire, ~50 km from Comox Burn, and with Douglas-fir plantations well established, Douglas-fir was the principal species eaten (31% by volume). Leaves and buds of salal, leaves and stems of red huckleberry and Oregon grape, leaves of bracken fern, and flowers of sedges were each taken at levels between 6% and 18%. Fifteen species were recorded, most providing less than 5% of the diet. These nesting females, on nearby areas, had rather striking differences in their diets, differences that likely resulted in part from reduced availability of some species, e.g., Douglas-fir at Comox Burn. Douglas-fir appears to have been selected for at Middle Quinsam because salal, willow, and bracken fern, although readily available, were used much less than at Comox.

Standing (1960) examined food habits of *D.o. pallidus* on a monthly basis in the Methow Valley. His monthly sample sizes were relatively small but illustrate the changing diet in spring and summer. His spring samples, April and May, included yearlings and adults of both sexes and were from plant communities ranging from Daubenmire's (1946) Douglas-fir Zone downward to, and including, the Wheatgrass–bluegrass zone.

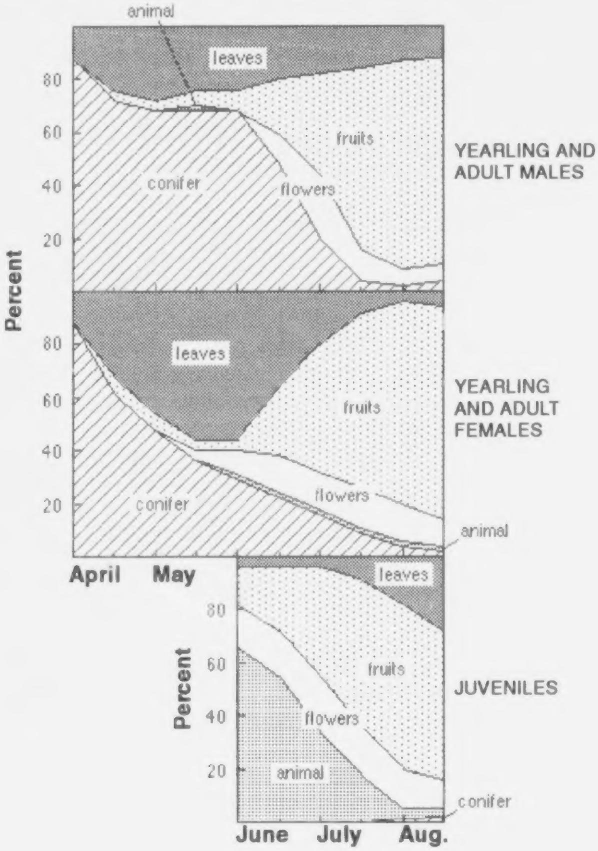
In April, Standing identified >25 species of plants that were eaten, among which only three exceeded 4% in terms of volume. Dandelion, at 40%, dominated the diet (Table 12.2). Many species were likely newly emerging and sparsely distributed, with low availability accounting for the wide diversity. Animal foods, ants and spiders, were negligible. In May, among >21 species of plants, only six exceeded 4% by volume, with only dandelion common to April and May. Dandelion and cudweed (*Gnaphalium* sp.) accounted for 47% of the total volume. Conifers, Douglas-fir and ponderosa pine, contributed 14%. Animal food was highest of any spring or summer month. Three crops with large numbers of carabid beetles (Carabidae) were mainly responsible for the high numbers of invertebrates.

Needles and staminate cones of ponderosa pine comprised 79% of the crop contents of 12 adult males in spring samples from Montana, with dandelion, at 8%, the only other species exceeding 5% (Schladweiler 1975). Among 12 adult females, ponderosa pine accounted for only 9% of crop contents, with dandelion at 27%, buttercup (*Ranunculus* spp.) at 17%, *Lithophragma* sp. at 11%, and pussytoes at 6%. As on Vancouver Island, females were taking much more herbaceous material than males.

(c) *Summer*. The summer diet also may vary among sex and age classes. Territorial males on Vancouver Island clear-cuts take much coniferous vegetation to at least the end of June (Fig. 12.4), by which time many males abandon their territories. Herbaceous plants figure heavily in the diet, and the few males that remain on breeding range throughout summer may shift heavily to fruits. Females fed heavily on herbaceous plants and leaves of deciduous shrubs but took conifer needles in moderate quantity. As fleshy fruits ripened, they were most used and the proportion of conifers declined. In subalpine Vancouver Island, the picture for males is similar to that on lowland clear-cuts, but females tended to take fewer fruits and more herbaceous material than in the lowlands (Figs. 1 and 2 of King 1973). Animal matter is negligible in summer diets of males and females on Vancouver Island (Fowle 1960; King and Bendell 1982; King 1973), as suggested by Stewart (1944) for coastal adults in general.

The summer diet of interior males includes a great variety of plant species; leaves and flowers of broad-leaved herbs, leaves, fruits, and seeds of herbaceous and woody plants, and considerable animal matter; with a concomitant decline in

Fig. 12.4. Principal classes of foods eaten by yearling and adult males, yearling and adult females, and juveniles on early forest seres on Vancouver Island. Adapted and modified (curves smoothed) from Fig. 1 of King and Bendell (1982).



coniferous material (Stewart 1944). Crop contents of 15 adult males in Montana included 21% coniferous, 20% shrub, 39% herbaceous, and 20% animal material (Schladweiler 1975). Those of 28 adult females included 8% coniferous, 8% shrub, 61% herbaceous, and 23% animal material. The greater use of animal matter by interior than coastal birds likely reflects differences in availability of insects, especially grasshoppers.

In contrast to adults, chicks feed heavily on invertebrates, mainly insects, in their first weeks, in some areas shifting soon to mainly fruits, leaves, and flowers (Figs. 12.3 and 12.4). They take small amounts of conifer needles in August. Although sample size was small, six chicks in subalpine Vancouver Island took less animal matter than in the lowlands, with shrubs and herbs contributing most food (Fig. 3 of King 1973). This may reflect a lower availability of invertebrates in the subalpine.

As in spring, summer is a period of rapidly changing availability. The major contrasts with spring are that many plants are dying or becoming dormant, and fruits of others are maturing, some with short, others long, seasonal availability.

Beer (1943) documented a wide variety of summer foods. In interior birds, leaves and buds of trembling aspen were eaten, mainly in early summer. Small amounts of wild buckwheat, clover (*Trifolium* spp.), and seeds of lupine were taken. Currants were a major food when ripe and serviceberries in July and August (they ripen about the time currants are ending). Chokecherries, rose hips, and snowberries were considered less preferred; the latter likely used in quantity only in the absence of other fruits (Beer 1943). In coastal areas, fruits of *Rubus* spp. and salal were considered preferred foods but were available in only limited quantities on interior ranges (salal not at all). Bearberries (*Arctostaphylos uva-ursi*) were consumed wherever found. Leaves, flowers, and fruits of huckleberries were widely used throughout summer, if available. Seeds of balsamroot were taken in quantity in June and July. Other Compositae taken occasionally were dandelion, false dandelion (*Agoseris* sp.), arnica (*Arnica* sp.), and fleabane. Dwarf mistletoe was eaten in small amounts when birds were feeding on its host plants, and western larch (*Larix occidentalis*) was a common food beginning in late August. White-bark and ponderosa pine were taken in small amounts in July and August. Insects, mainly ants (Formicidae), beetles (Coleoptera), and grasshoppers dominated animal foods in summer, mainly by juveniles. Insects from eight orders, and occasional spiders (Araneida), millipedes (Diplopoda), and centipedes (Chilopoda) were eaten.

Stewart (1944) also found a wide variety of foods in the summer diet. He identified 19 kinds of fruits and seeds in early summer crops of interior birds, the more important of which ranked in importance as follows: bearberry > strawberry (*Fragaria* spp.) > currant. Major species from which green leaves were used were buckwheat > vetch (*Vicia* sp.) > willow > buffaloberry (*Shepherdia canadensis*) > dandelion. Flowers eaten in greatest quantity were cherry (*Prunus* sp.), buckwheat, pink microsteris (*Microsteris* sp.), dandelion, and false dandelion. Needles of conifers, especially pine, were taken in moderate amounts. Insects, mainly beetles, leafhoppers (Cicadellidae), and saw-fly larvae (Tenthredinidae) were eaten in "appreciable quantities"; ants, frequently, but never in quantity. In late summer, many fruits and seeds were eaten: blueberry > bearberry > pine > rose > cherry > serviceberry. Leaves continued to be consumed in large quantities, major species being buckwheat > willow > trembling aspen > blueberry. Needles of spruce, western larch, pine, and especially Douglas-fir were taken in small amounts. Principal animal foods were short-horned grasshoppers (Acrididae) and ants.

Stewart examined crop samples of 19 post-downy interior juveniles. Leaves of wild buckwheat, blueberry, dandelion, and cherry comprised approximately one-third of the diet; fruits and seeds of cherry, blueberry, bearberry, serviceberry, smartweed (*Polygonum* sp.), and currant, approximately one-third; and a variety of insects, mainly short-horned grasshoppers and ants, approximately one-third. A few needles of Douglas-fir were found.

A small sample of coastal birds in Stewart's collection indicated flowers were important in the early summer diet, especially those of hairy cat's ear. Those of salal and sheep sorel (*Rumex acetosella*) were taken in smaller amounts. Among leafy material, blueberry was most used, with smaller amounts of black medic (*Medicago lupulina*) and bracken fern. Most used fruits and seeds were blueberry > red elderberry (*Sambucus racemosa arborescens*) > bramble (*Rubus* sp.) > tarweed (*Madia* sp.). By late summer, fruits and seeds were most used, mainly blueberry, bearberry, bramble, and mountain ash (*Sorbus* sp.). Dominant leafy materials were blueberry, clover, ferns, buckwheat, and hawkweed. Small amounts of animal matter consisted mainly of short-horned grasshoppers, leaf beetles (Chrysomelidae), and ants.

On lowland clear-cuts on Vancouver Island, more than 80% of plant foods eaten in spring and summer consisted of eight species (King and Bendell 1982). In June, males ate large amounts of Douglas-fir; lesser quantities of leaves of willow, bracken fern, salal, red huckleberry, and clover; flowers of hairy cat's ear; and fruits of wild blackberry (*Rubus ursinus*), salal, and red huckleberry. Hens and chicks consumed the same species, but less Douglas-fir and more cat's ear. Some common species or groups were clearly avoided, e.g., fireweed and grasses. Chicks tended to eat fewer conifer needles and broad-leaved plants than males or females, concentrating on fruits of wild blackberry, salal, and red huckleberry. Ants, beetles, and spittle bugs (Cercopidae) were principal animal foods, with chicks taking them most frequently. Chicks also consumed a wider variety of invertebrate taxa than adults and that included Isopoda, Arachnida, Diptera, Lepidoptera, and Myriopoda, among others. Most invertebrate taxa were taken approximately as available but arachnids, dipterans, and lepidopterans less so. Invertebrate taxa recorded from adults but not chicks were Orthoptera, Diplopoda, and Gastropoda. Adults took invertebrates less frequently than available.

At Lower Quinsam, Stiven (1961) found arachnids, dipterans, and larval lepidopterans at a lower frequency in crop samples from small chicks than in samples he collected from the field ("available"). He thought this might reflect his being more efficient than chicks in finding these groups. However, since other taxa were found at about the same frequency in crops and field samples, it may reflect avoidance of these taxa by chicks.

The summer diet of adult males and females in subalpine Vancouver Island differed from that on nearby lowlands (King 1973). The switch from mainly coniferous to deciduous plants appeared in late May in females, ~1 month later than in the lowlands, and in June in males, as in the lowlands. The difference in time of switching in females corresponded with that found in egg-laying and hatch. Three species of huckleberry comprised ~70% of foods identified, more so in males than females. Females consumed more broad-leaved herbs, strawberries, and bearberries than males, and both took less coniferous matter than in the lowlands. A wide variety of deciduous species was eaten, most in small quantities. There was a clear selection for huckleberry by all grouse and avoidance of white rhododendron (*Rhododendron albiflorum*), copper-bush (*Cladothamnus pyroliflorus*), heaths, other shrubs, some herbs, and grasses. Chicks took mainly broad-leaved herbs in July, with huckleberry contributing ~25% to the diet. Huckleberry was the principal food in August, with broad-leaved herbs contributing ~20%. *Vaccinium* spp. was the principal deciduous species taken throughout the year. Animal matter was insignificant in the diet of older birds and comprised ~15% of that of chicks in July and August.

Standing (1960) collected samples in the Methow Valley from the Spruce–fir, Douglas-fir, Ponderosa pine, and Wheatgrass–bluegrass zones in June, July, and August. These samples are believed to be mainly, if not solely, from yearlings and adults, but this is not clear in his presentation and samples from a few larger juveniles may be included.

Table 12.2. Monthly diet (% volume, mL) in spring and summer in the Methow Valley.

	April	May	June	July	August
PRINCIPAL PLANTS					
Common dandelion	40	26			
Grasses (various)	27				
Creamy buckwheat[a]	17				
Trembling aspen		8			
Cudweed		21			
Ponderosa pine		5			
Douglas-fir		9	11		7
Balsamroot			16		
Yellow salsify			45	10	24
Western larch			7	10	
Blue-eyed Mary[b]			6		
Serviceberry				57	37
Engelmann spruce				6	
Prickly lettuce[c]					11
Chokecherry					16
Subalpine fir					14
Total no. of species	>25	>21	>15	>13	12
Animal food	<1	12	2	4	7
No. of samples (crops)	31	19	11	13	11
Total volume	234	115	191	91	412

Note: Only plants contributing ≥5% are included (extrapolated from data in Standing (1960)).

[a] *Eriogonum heracleoides.*

[b] *Collinsia parviflora.*

[c] *Lactuca serriola.*

As in spring, principal species consumed changed from month to month (Table 12.2). Seeds of balsamroot and leaves and flowers of yellow salsify (*Tragopogon dubius*) dominated the diet in June; fruits of serviceberry were dominant in July and August. No conifer needles were recorded in July, but by August both Douglas-fir and subalpine fir were found. Beetles were the principal invertebrates taken in June; ants, in July; and grasshoppers in August. In view of Standings' relatively small monthly samples, one must use caution in their interpretation, for collecting locations may have affected his results. Nevertheless, changes across monthly samples generally parallel what is known about the phenology of plants in the areas in which he worked. Standing noted that some birds move through various vegetation zones in summer, and that this will affect species available to them.

Among adult males from Montana, 15 summer crops contained 15% ponderosa pine, 6% Douglas-fir, 10% buffaloberry, 7% sticky laurel (*Ceanothus velutinus*), 18% strawberry, 7% yellow salsify, and 8% dandelion (Schladweiler 1975). Among adult females, 28 crops contained 7% Douglas-fir, 12% strawberry, 27% yellow salsify, and 7% clover. As in spring, here and on Vancouver Island (King 1973; King and Bendell 1982), females consumed less coniferous matter than males.

Schladweiler (1975) examined crop contents of 48 Montana juveniles in June, July, and August (26 were <1–4 weeks of age, the remainder 5–8 weeks of age). Among the younger birds, crops contained 64% orthopterans, 6% lepidopterans, and 17% herbaceous matter, of which 11% was dandelion. Among the older birds, 74% was orthopterans, 10% shrub, and 10% herbaceous matter, with no single species exceeding 5%. Invertebrates were used heavily throughout summer.

Foods of birds that leave summer range early, yearling and adult males and non-breeding and unsuccessful females, are not well known but must vary with plant communities through which they pass and foods available where they settle. These birds may include more coniferous vegetation in their diets than in those remaining on lowland range, but this is speculative.

(d) *Autumn*. Many birds are on the move toward winter range, passing through various plant communities. Others have settled on winter range, but availability of particular species of plants is changing (fruits of some are gone or past prime, and leaves of others are being shed or desiccating and, presumably, changing in palatability).

Fruits (Fowle 1960), leaves, and flowers continued to dominate the diets of hens and chicks on Vancouver Island in September, in that relative order of importance (Figs. 1B and 1C of King and Bendell 1982). Conifer needles and animal matter were negligible, the former increasing slightly, the latter decreasing as the month progressed. In contrast, Beer's (1943) analyses for blue grouse in general (Figs. 12.2 and 12.3) suggested a relatively high use of conifers and miscellaneous plants in September, with few fruits taken. Samples from Vancouver Island were mainly from early forest seres where coniferous vegetation was readily available, suggesting fruits are preferred. King and Braun (1970) suggested that fruits and herbs are a preferred autumn food of blue grouse in alpine Colorado and analyses from subalpine Vancouver Island agree (King 1973). The strong shift to conifers indicated by Beer's data indicate that fruits may not be available in many areas by early autumn or may reflect the areas from which he collected samples. By October and, especially, November, Beer's data indicated that birds were feeding primarily on conifers, the staple winter diet.

There are other studies of autumn foods from the analysis of crop contents of grouse shot by hunters. The diet composed of coniferous vegetation varied markedly among areas (Table 12.3). In general, populations in northern interior areas (i.e., interior WA (Boag 1963); ID–OR–WA (Beer 1943)) were feeding mainly on conifer needles. Farther south, fruits, leaves, and flowers comprised the principal foods eaten. These data indicate blue grouse selected the latter foods if given a choice and shifted to needles secondarily. That shift may take place well before low-growing terrestrial plants are covered by snow (in ID–OR–WA persistent snow does not usually occur until late October or November, even at many upper elevations).

Table 12.3. Amount of conifer in the autumn diet (%) and principal types of autumn foods of blue grouse in various parts of their range.

Subspecies	Area	Period	% conifer	Principal food type[a]	Source[b]
obscurus	AZ	September	10	L, Fl	1
obscurus	CO	Autumn	10	L, Fr	2
pallidus	OR	Aug.–Sept.	6	A	3
pallidus	MT	Sept.–Nov.	11–44[c]	L, Fr	4
pallidus	WA	Sept.–Oct.	78–97[d]	N	5
fuliginosus	WA	Sept.–Nov.	16	Fr	6
fuliginosus	BC	September	<3[e]	Fr	7
fuliginosus	BC[f]	Autumn	~2[g]	Fr	8
fuliginosus	BC[f]	Autumn	~22[h]	Misc.	8
Interior[i]	Various	Autumn	51	N	9
Coast[i]	Various	Autumn	0	Fr	9
Various[j]	ID–OR–WA	Sept.	~52[k]	N	10
		Oct.	~80[k]	N	10
		Nov.	~100[k]	N	10

[a] A, animal; Fl, flowers; Fr, fruits; L, leaves of deciduous and herbaceous plants; N, conifer needles; misc., non-coniferous.

[b] 1, LeCount 1970; 2, King and Braun (1970); 3, Crawford et al. (1986); 4, Schladweiler (1975); 5, Boag (1963); 6, Dragness (1968); 7, King and Bendell (1982); 8, King (1973); 9, Stewart (1944); 10, Beer (1943).

[c] Range among four areas.

[d] Annual range among years, 1958–1961.

[e] Extrapolated from King and Bendell's Figs. 1B (adult females) and 1C (juveniles).

[f] Subalpine population.

[g] Extrapolated from King's Fig. 1 (adult males).

[h] Extrapolated from King's Fig. 12 (adult females).

[i] Mixtures of interior and coastal subspecies from various parts of ranges, respectively.

[j] Includes mixture of *D.o. pallidus* and *D.o. fuliginosus*.

[k] Extrapolated from Beer's Fig. 3 (adults).

Table 12.4. Notable species, or groups of species, of plants identified in 10 studies of autumn food habits of blue grouse.

Species or group	Region (sources)[a]
Blueberry and huckleberry	1, 2, 3, 4, 5, 6, 7
Douglas-fir and true firs	1, 2, 3, 4, 6, 7, 8
Dandelion	1, 3, 4, 7, 9
Clover	2, 4, 5, 7, 9
Wild buckwheat	1, 7, 8, 10
Pine	1, 4, 6, 7
Willow	5, 6, 9
Western larch	1, 7, 8
Bearberry	1, 4, 7
Rubus spp.	3, 5
Oregon grape	1, 4
Salal	2, 5

[a] 1, northcentral Washington (Boag 1963); 2, coastal Washington (Dragness 1968); 3, eastcentral Arizona (LeCount 1970); 4, southeastern Wyoming (Harju 1974); 5, Vancouver Island (King and Bendell 1982); 6, composite sample from throughout range (Stewart 1944); 7, western Montana (Schladweiler 1975); 8, composite sample from Washington (Beer 1943); 9, subalpine Colorado (King and Braun 1970); 10, northeastern Oregon (Crawford et al. 1986).

We examined autumn food habits as reported by 10 authors who identified species or groups that might be considered major foods. Blueberries and huckleberries and Douglas-fir and true firs headed the list in terms of occurrence among studies (Table 12.4). Twelve species, or species groups, were conspicuous items in two or more studies. A number of other species or groups were conspicuous only once, among them juniper, cat's ear, yellow salsify, pussytoes, vetch (*Vicia* sp.), elderberry (*Sambucus* spp.), Oregon grape, alum-root, chickweed, hawthorn (*Crataegus* sp.), serviceberry, snowberry, mountain ash, trembling aspen, and ferns. It is clear from studies considered that one species, or group, of plants was most heavily used in autumn in each area: in northcentral Washington, western larch (Boag 1963); in coastal Washington (Dragness 1968) and on lowland Vancouver Island (King and Bendell 1982), salal; in subalpine Vancouver Island, huckleberry (King (1973); in subalpine Colorado, clover (King and Braun 1970); in Arizona, vetch (LeCount 1970); in Wyoming, lodgepole pine (Harju 1974); and in both Stewart's (1944) and Beer's (1943) composite samples, Douglas-fir and true firs. The most surprising dominant autumn food ($n = 83$ crops from northeastern Oregon) was short-horned grasshoppers, comprising 32% of the total sample by mass (Crawford et al. 1986*b*). At least 19 taxa of insects and some spiders were identified, all but three in trace amounts.

(e) *Animal foods—a summary of taxa.* A wide variety of animal foods have been recorded in diets of blue grouse, mainly insects. Individuals from at least 11 orders and 30 families have been identified (Beer 1943; Stewart 1943; Fowle 1960; Standing 1960; Stiven 1961; Boag 1963; Dragness 1968; King and Braun 1970; LeCount 1970; King 1973; King and Bendell 1982; Crawford et al. 1986*b*). Ants were most often reported, usually in low volume; various beetles frequently, sometimes in moderate volume; and grasshoppers, frequently and in greatest volume. Weber (1975) found animal foods to make up 68% ($n = 5$ crops), 88% ($n = 31$), 62% ($n = 26$), and 28% ($n = 6$) of the contents of juvenile crops collected in June, July, August, and September, respectively. Lepidopteran larvae were most important in June, grasshoppers in all other months. Most insects eaten by blue grouse tend to be "fairly large" (Beer 1943, p. 40), and some smaller individuals may be ingested in conjunction with other foods.

Spiders (Araneidae) are commonly found in food samples. Isopods (Isopoda), chilopods (Chilopoda), diplopods (Diplopoda), and gastropods (Gastropoda) are occasionally found, none in large amounts. Perhaps the most exotic animal food reported was two newly born northern alligator lizards (*Elgaria coerulea*), 85 and 90 mm in length, respectively. These were found in the crop of an adult male shot on Mount Shasta, CA (Simons 1986).

12.1.3 The basis for selection

Two criteria are most often proposed as the basis for selection, or avoidance, of particular foods by blue grouse: (1) *nutritional quality* (Wing 1947; King and Bendell 1982; Stauffer and Peterson 1986; Cade and Hoffman 1990; Remington 1990) and (2) *toxic chemical compounds* (Bryant and Kuropat 1980; Remington 1990), so-called "secondary compounds". Interactions among factors may complicate attempts to identify causes for selection (Robbins et al. 1987), and most studies of this grouse have involved only measurements of amounts of the more common nutrients in plant samples (Hoffmann 1961; Boag and Kiceniuk 1968; King and Bendell 1982). Secondary compounds (in plants eaten by other grouse) have most often been studied by measuring their concentrations within food plants (Remington and Braun 1985; Hupp 1987; Servello et al. 1987; Jakubas et al. 1989). Without parallel bioassays, these studies may be misleading (Remington 1990). Nevertheless, in most cases, this is all we have.

(a) *Nutrients as a basis for selection.* King and Bendell (1982) measured various nutrients in plants and animals used as food on spring and summer range on Vancouver Island. Plant foods used in March and April were high in fat, ash, N, and K; and in July and August, in ash, K, and perhaps N. Flowers of cat's ear were heavily used by all sex and age classes of birds and were higher in fat, ash, N, P, K, Mg, and Na than were flowers of salal, which were rarely eaten. King and Bendell suggested these data support an argument for a nutritional basis to food selection. They found no such relationship between used and unused berries and invertebrates and thought that their use may be based on nutrients not examined, or other factors. They noted the difficulty in attempting to identify what specific nutrients might be involved in selection but proposed that high levels of fat, N, P, and K might be important in the choice of foods by chicks, and of ash, N, and K, by adults.

Hoffmann (1961) analysed crude protein content of white fir needles from winter roost trees in the eastcentral Sierra Nevada. Needles collected at ~3 m high averaged 4%–5% protein, those at ~15 m, 6%–7%, a "strongly significant" difference between samples. Most feeding was at upper levels of the trees. Hoffmann concluded that protein might be the basis on which selection was based but noted that other factors, e.g., microclimate, could have influenced parts of the trees used.

Needles of lodgepole pine are a primary winter food in southwest Alberta (Boag 1964). Here, Boag and Kiceniuk (1968) found a much lower crude protein content in needles from crops of two blue grouse (0.48%) than in needles collected from trees at the same site (3.15%). They concluded these birds were not selecting needles on the basis of protein content.

Remington (1990) is the only person to have conducted nutritional bioassays with blue grouse (see 12.2). Neither crude protein nor neutral detergent fibre (NDF) were linked to species preferences. Douglas-fir, although preferred, ranked fourth in crude protein content among five species of conifers tested, and needles from older Douglas-fir trees contained more NDF than those from younger trees, but were strongly preferred.

Remington (1990) also conducted "needle-age trials" with Douglas-fir. Different aged needles were offered to birds after having been removed from branches. There was a strong selection for 1–2 year-old needles over those up to 6 years of age, suggesting selection was not related to positional cues within trees or branches. Interestingly, preference declined between needle ages 1–2 and 3–4; crude protein, between ages 3–4 and 5–6. Metabolizable energy (ME) did not differ among age classes of needles but tended to decline with age. Metabolizable nitrogen (MN) declined with needle age.

(b) *Secondary compounds as a basis for selection.* Secondary compounds may work in two ways to deter feeding: (1) directly, as toxicants, or (2) indirectly, through costs of detoxification (Remington 1990). Remington conducted studies of such "anti-nutrients" and their relation to food selection with captive birds. He worked with five species of conifers considered as potential winter foods in Colorado: Douglas-fir, lodgepole pine, subalpine fir, and Engelmann spruce, and to a lesser extent, with limber pine.

Conifer needles contained from 0.5% to 2.4% (dry mass) monoterpenes, but neither monoterpene composition nor content was related to preference. Douglas-fir contained more than twice the monoterpene content of limber pine and Engelmann spruce, but was more preferred. Addition of monoterpenes to Douglas-fir needles did not appear to reduce, may have even increased, their digestibility. Remington concluded (p. 30), "differences in palatability, metabolizable energy, and metabolizable nitrogen among needle age groups [of Douglas-fir] were not consistently related to differences in . . . tannin activity, or monoterpene content."

The energy cost of detoxification ranged from 1% to 10% of ME, the nitrogen cost, 34% to 69% of ingested nitrogen in needles of the four principal species. Remington suggested there is a substantial energy and nitrogen cost associated with detoxification of secondary compounds and that deterred feeding on some species may represent an opportunity cost in terms of energy and nutrients not ingested. Overall, he concluded (p. 19), ". . . no single chemical parameter is driving blue grouse food selection."

(c) *Other criteria as a basis for selection.* King and Bendell (1982) suggested that such things as availability of alternate foods, intra- and inter-specific interaction, a need for roughage, and the ease of gleaning food may affect selection, but these suggestions require further study.

Others have noted that within specific taxa, blue grouse appear to select particular trees for feeding and (or) roosting in winter; e.g., a selective use of dwarf or stunted trees near timberline, or, at lower elevations, larger trees within a stand (Wing 1947; Cade and Hoffman 1990; Remington 1990), large trees with heavy foliage (Caswell 1954*b*; Stauffer and Peterson 1986), larger trees within parkland (King 1971), or Douglas-firs with atypical or stressed growth patterns (Remington 1990; Pekins et al. 1991). Criteria suggested for choice are as follows: nutritional advantages (Wing 1947; Stauffer and Peterson 1986; Cade and Hoffman 1990; Remington 1990); physical advantages, e.g., strong limbs allow ease of movement for a heavy-bodied bird (Wing 1947; King 1971); favourable microclimate (Wing 1947; King 1971; Cade and Hoffman 1990; Pekins et al. 1991), and protection from predators (Cade and Hoffman 1990). Cade and Hoffman considered nutritional advantages as most important and suggested that protection from weather and predators are unlikely reasons for a selective use of feeding trees on winter range. None of the above has been adequately tested.

Criteria for selection often are not clear. Some not suggested above may be involved, e.g., moisture content of the plant, dispersion and juxtaposition to other items within a plant community, perhaps, even taste. Robbins (1983) has noted the extreme difficulty in identifying specific reasons for selection of a particular food. He concluded (p. 324) that most workers have based their suggestions on correlations but that ". . . the cause–effect basis of food habits is far more complex than significant, or even insignificant, correlations."

12.2 Nutrition

As with most species of animals in the wild, specific nutritional requirements of blue grouse are not known (King and Bendell 1982). In fact, there is no empirical information on even their gross daily food consumption in the wild. Stiven (1961), however, estimated mean daily food requirements (fresh mass) of 1–4-week-old chicks with the factorial method (Maynard and Loosli 1956). Chicks were estimated to need 15.5, 32.4, 61.1, and 130.1 g/day, each week of age, respectively. The only other estimates of daily food consumption of blue grouse were derived from two adult males and two adult females on a winter diet of Douglas-fir in captivity. Males consumed 93.8 ± 0.97 g dry matter (wet mass = 187.7 ± 1.85 g)/(bird day); females, 79.4 ± 1.21 g dry matter (wet mass = 151.3 ± 2.31 g)/(bird day) (calculated from data provided by TE Remington and in Remington 1990).

Most nutritional work with blue grouse has involved field studies in which some nutritional requirements have been presumed from work with domestic poultry.[5] Three types of studies have been reported: (1) those involving proximate chemical analyses of foods eaten, or of plant parts or invertebrates collected to simulate feeding, (2) one study involving bioassays of digestibility of selected winter foods, and (3) population level studies involving comparisons among areas or between fertilized and unfertilized plots. Population level studies will be considered in a future publication.

12.2.1 Proximate chemical analyses of grouse foods

Stiven (1961) analysed seven groups of invertebrates eaten by young blue grouse, and seven commonly eaten species of

Table 12.5. Nutrient composition (% dry weight) and its digestible portion of invertebrates and plants commonly used as food by chicks at Middle Quinsam.

Type of food and its chemical composition	Percent dry weight[a]	Digestible portion
INVERTEBRATES[b]		
Crude protein	69.3	58.8
Ether extract	3.8	3.2
Nitrogen-free extract	16.7	11.0
Crude fiber	6.0	1.2
Ash	4.1	
Moisture	65%	
PLANTS[c]		
Crude protein	11.6	7.6
Ether extract	3.3	1.8
Nitrogen-free extract	56.9	37.0
Crude fiber	18.6	6.0
Ash	9.6	
Moisture	74%	

Note: Calculated from data in Stiven (1961).

[a] Except moisture.

[b] Mean composition of seven commonly eaten groups of invertebrates.

[c] Mean composition of six species and one genera (*Salix* spp.) of commonly eaten plants.

plants (*Salix* spp. considered as one species), for crude protein, ether extract, nitrogen-free extract, crude fibre, and ash (% dry mass) at Middle Quinsam. These values showed a much higher protein content, and much lower carbohydrate content, in animal foods than in plants (Table 12.5), a generally recognized relationship. A requirement for high amounts of protein (>20%) is sometimes quoted as the basis for selection of invertebrates by young, rapidly growing tetraonines (Pendergast 1969; Spidsø 1980; Myrberget 1981).

On the basis of average digestibilities of animal and plant foods by chickens (Titus 1949), Stiven estimated the digestible portions of each of the nutrients for each group of invertebrates and each species of plant. We computed mean digestible portions for each nutrient for combined invertebrate and combined plant foods from data in Stiven (Table 12.5).

King and Bendell (1982) conducted proximate analyses of common foods from summer range at Middle Quinsam. From these, they calculated "nutritional quality" of the diet by season for males, females, and chicks (Table 12.6). They concluded the following: (1) in March and April, diets of males and females were, overall, of similar quality; (2) in May and June, the diet of females was richer in ash, N, and Mg than that of males; (3) in July and August, the diets of males and females were similar in quality; and (4) diets of females were slightly higher in Ca than in males in all periods. The diet of chicks in May and June appeared to be lower than that of adults in carbohydrates, fat, and Ca, but higher in N, P, and K, much higher in N. By late summer that of chicks was approaching that of adults in overall quality but was still higher in N. These data represent plants on summer range and were not adjusted for digestibility, a relatively unknown quantity for blue grouse.

Considerable attention has been focussed on winter foods of blue grouse, principally because conifer needles form nearly their entire diet at this time and because of a presumption that needles are of poor nutritional quality. As noted in 12.1.3, Hoffmann (1961), in the Sierra Nevada, found crude protein content in needles of white fir, the principal winter food of blue grouse in that area, to range between 4% and 7%, and highest at upper tree levels. It did not vary seasonally or among years.

Crude protein of lodgepole pine needles in southwestern Alberta, a primary winter food there, averaged 4.52% (% dry mass; range = 0.10–8.40%) in 111 samples taken in May, July, and November, with no difference among seasons (Boag and Kiceniuk 1968). There were no significant differences in crude protein between needles collected at low (1740 m; 4.96%) and high (1920 m; 3.02%) elevations or from young (<15 years of

Table 12.6. Major nutrients/100 g dry mass of crop contents of grouse on Vancouver Island (adapted from Table 9 of King and Bendell (1982)).

	CHO[a]	Fat	Ash	Crude protein[b]	P	K	Ca	Mg
MARCH–APRIL								
Males	75.0	14.0	3.0	8.75	0.20	0.50	0.60	0.20
Females	77.0	13.0	3.0	8.75	0.20	0.50	0.70	0.20
MAY–JUNE								
Males	73.0	13.0	4.0	13.75	0.30	1.00	0.50	0.10
Female	70.0	10.0	6.0	16.25	0.30	1.00	0.60	0.20
Chicks	44.0	4.0	7.0	45.63	0.73	2.00	0.30	0.30
JULY–AUGUST								
Males	78.0	4.0	7.0	10.00	0.40	1.60	0.30	0.20
Females	79.0	4.0	6.0	10.00	0.30	1.50	0.40	0.20
Chicks	70.0	4.0	7.0	19.38	0.50	1.70	0.30	0.20

[a] Carbohydrate.

[b] N × 6.25.

age; 3.11%) and older (>15 years of age; 4.52%) trees. Crude protein was significantly greater in a stand of pine ~88 years after fire (6.5%) than in stands 20 (5.80%) and 32 (5.85%) years after fire, and in needles from trees growing on river terraces as compared to those on mountain slopes. Clearly, crude protein levels of needles of both white fir and lodgepole pine were low relative to foods taken at other seasons (Table 12.6).

12.2.2 *Bioassays of digestibility*

Much concern about the digestion of tetraonines has centred around their highly fibrous winter diets and the possible role of the ceca in the utilization of these foods (Leopold 1953; McBee and West 1969; Fenna and Boag 1974; Moss 1983); so, too, with blue grouse.

Remington (1990) studied digestibility of selected winter foods with captive birds in Colorado. Percent metabolizable nitrogen (MN) varied among species and followed the rank order: Douglas-fir = lodgepole pine > subalpine fir > Engelmann spruce. Metabolizable nitrogen was greater in old than young Douglas-firs, especially within 1–2-year-old needles and declined as needle age increased. Birds maintained a positive nitrogen balance only on 1–2-year-old needles of Douglas-fir. Nevertheless, winter diets of some populations of blue grouse may be largely, perhaps solely, composed of pines (Zwickel and Bendell 1986), true firs (Beer 1943; Hoffmann 1961), or hemlocks (King 1971; Hines 1987), so more work is needed on this subject. Suboptimal nitrogen levels in some conifers may be compensated for by increased consumption and (or) recycling of nutrients, for blue grouse maintain themselves and may gain mass on a variety of species in the wild.

Remington (1989) also examined the digestibility of neutral detergent fibre (NDF) in needles of Douglas-fir, lodgepole pine, subalpine fir, and Engelmann spruce. Digestibility ranged from 7.5% to 17.3% among species, subalpine fir highest, Engelmann spruce lowest, and averaged 13.0% for all species combined. Digestibility was high for particles that entered the ceca, averaging 96.8% among the four species (range = 94.3%–98.6%). Remington proposed that exclusion of NDF from the ceca, and, to a lesser extent, efficiency of fermentation, affect its total digestibility. He reported that among the tetraonines, blue grouse have relatively short ceca and a high-fibre diet, a contradiction to the cecal fibre digestion hypothesis. Moss (1983) concluded, on the basis of theoretical calculations based on gut lengths and body mass, that three of the tetraonines that eat mostly conifer needles in winter—capercaillie, blue grouse, and spruce grouse—have low digestive abilities.

Both Moss (1983) and Remington (1990) stressed that digestibility is in part a property of the eater and that this must be considered in evaluations of food quality. Remington (p. 41) concluded, "Palatability of, and performance . . . on, species or age groups of needles . . . was not consistently related to chemical measures of food quality." He suggested (p. 31), "It is unlikely that measures of nutrients or secondary compounds within winter foods of grouse will allow meaningful assessments of the true value of that food." We also believe quality is partly a property of the eater, and if so, although conifer needles appear low in quality relative to conventional wisdom, at least some are a high-quality winter diet for tetraonines adapted to use them.

12.3 Water

Water is essential for life, and most of that used by the individual is ingested in its free form or as a component of food (Maynard and Loosli 1962). Access to free water, or succulent foods, is thus a potential limiting factor for occupation of an area by an individual or species.

12.3.1 *Use*

(a) *In the aviary*. Stirling (1965) provided information on water consumption by captive birds. He measured water used by grouse held on a chicken breeder ration for 19–20 days in an indoor aviary. These birds, with a mean body mass of 923 g, drank, on average, 48.9 mL of water/day, 5.3 mL/100 g of body mass. We once held blue and ruffed grouse from Vancouver Island on a chicken breeder ration in a covered outdoor aviary and estimated, on the basis of general observations, that ruffed grouse drank about twice as much water per body mass as blue grouse (Bendell and Elliott 1966).

Bump et al. (1947) calculated daily water consumption for ruffed grouse held on a maintenance diet as 22.6–26.0 mL/day. After correcting moisture content of their maintenance diet to equate with a commercial breeder ration, we calculated that ruffed grouse (at a mean mass of 539 g, from data in their Table 116) would consume ~43 mL of water/(bird day), 8 mL/100 g of body mass. Compared to blue grouse held by Stirling (1965), ruffed grouse would consume about 1.5 times as much water per body mass as blue grouse rather than twice as much, as we once estimated.[6]

(b) *In the field*. There has been considerable speculation as to the need for free water by wild blue grouse, but few data are available. Access to water might be most critical on dry interior ranges, and although wild blue grouse there drink (Beer 1943; Wing et al. 1944; Caswell 1954*b*; Henderson 1960), such observations are rare. Movements into creek bottoms and to water holes or springs, especially by broods, may be for water (Wing et al. 1944; Marshall 1946; Schottelius 1951*a*; Henderson 1960). Wing (1947) suggested that if water sources dry up on dry ranges this may spell the difference between success and failure of a local population. Bauer (1962) felt poor production on his study area in one year was related to local drought and drying of springs and ponds by early July. In contrast, Weber (1975) noted no evident connection between territories of males or movements of broods and areas with free water on shrub-steppe breeding range in Utah. He thought broods may be attracted to mesic areas for such things as insects or cover. Broods were never seen at either of only two sources of free water on Hoffman's (1981) Green Mountain study area in Colorado. And, in northcentral Washington, although females and young aggregated in and around aspen thickets on shrub-steppe range in July and August, more often than not they were in those without open water (Zwickel 1973). On Vancouver Island, Fowle (1960) never saw blue grouse drinking in the field, and on only three occasions in captive birds. Here, also, Bendell (1954) suggested that free water bore no relationship to movements of hens and broods. Succulent foods in coastal areas, especially berries, may preclude the need for free water (Fowle 1960; Armleder 1980). This may be true even on interior ranges if succulents are available (Beer 1943; Wing et al. 1944; Weber 1975).

Other evidence also suggests open water may not be critical for at least some birds. In heavily banded populations, territorial males are rarely, if ever, found off their territories in the peak breeding period, even though many territories provide no access to open water. Wing et al. (1940) and Marshall (1946) noted that birds at higher elevations are often far from water when compared to hens and broods at lower elevations in the same general region. Temperatures at higher elevations would be cooler, and these areas might have a more dependable supply of succulent vegetation.

At Liberty, UT, most nests of blue grouse were located within 400 m of open water (Weber 1975), indicating access to water could be critical for nesting. We found the median distance of 435 nests in young coast forest in British Columbia to be 50 m from the nearest water (<1–550 m). Within this sample, 49% were ≥100 m, 19% ≥200 m, 5% ≥300 m, and 1% ≥400 m from water. The median distance from free water of 24 nests in shrub-steppe range in northcentral Washington was 150 m (10–800 m). Within this sample, 62% were ≥100 m, 41% ≥200 m, 29% ≥300 m, and 21% ≥400 m from water. Nests were significantly farther away, on average, in the dry interior area than in coastal British Columbia [2]. Nesting success at the two areas did not differ [3], indicating distance from water likely had no effect on this parameter.

12.3.2 Sources

There are a number of potential sources of water, e.g., succulent herbs, berries and other fruits, insects and other animal foods, dew, rain-wet vegetation, and snow, as well as creeks, springs, ponds, and temporary water catchments. Berries, other fruits, and invertebrates tend to be most available in mid and late summer, periods when open water is most scarce. We suspect moisture requirements of blue grouse are filled principally from ingested food in spring and summer and that water is not a problem in winter because of the availability of snow and (or) free water on most winter ranges. As well, the broken topography of most occupied areas provides alternating ridges and gullies, often with creeks or springs in gullies or on sides of ridges. Access to free water is probably not a serious problem on most occupied ranges. Ruffed grouse, too, are thought by some to be relatively independent of a need for free water (Bump et al. 1947; Edminster 1947; Barber et al. 1989), even though their moisture requirements appear greater than those of blue grouse.

12.3.3 Water as a limit to distribution

Although water does not seem to be a major problem on most occupied breeding ranges, southern areas at low elevations tend to have xeric vegetation (low succulence) and depauperate invertebrate populations, with drought-like conditions in mid to late summer. Desiccation of vegetation has been suggested as a possible cause of early migration from some breeding ranges, even farther north (Musschl 1960; Bendell and Elliott 1967). Low moisture, either in foods or as free water, might limit distribution at the southern end of the range of blue grouse, and a more detailed examination of this question is warranted.

12.4 Grit

Small stones are eaten by many birds, including most grouse (except, perhaps, sage-grouse (Patterson 1952)). These stones, grit, accumulate in the gizzard and aid in the mastication of food, especially more fibrous food.[7] Some have suggested grit is required by tetraonines (in blue grouse, Boag 1958), that a shortage in winter may cause severe mortality (in ptarmigan, Siivonen 1962), or that a shortage may be a limiting factor at the population level (grouse in general, Welty 1964). While its function as an agent of mastication seems clear, some have proposed that it also may be an important source of dietary minerals (McCann 1939; Labisky et al. 1964; Pendergast 1969; King and Bendell 1982; Bendell-Young and Bendell 1999, among others). The latter has been postulated as a principal function in ring-necked pheasants in some areas (McCann 1939), and in Norwegian willow ptarmigan in some seasons (Norris et al. 1975).

12.4.1 In the crop

Grit is commonly reported from crops of blue grouse, always in small quantities (Table 12.7). Although data are limited, it tends to be more common in crops in late summer and fall than in spring and early summer. For example, King and Bendell (1982) found a greater frequency of occurrence in August and September (19.7%) than in March through July (8.4%). Since it is never found in large quantities, and some 75% or more of all crops contain none, it may pass on to the gizzard rather rapidly, perhaps differentially in relation to other items.

12.4.2 In the gizzard

The gizzard of blue grouse, as a point of accumulation, almost always contains stones and in much greater frequencies and quantities than in the crop (Table 12.7).

(a) *In chicks.* Newly hatched chicks eat stones almost immediately on leaving the nest. Among 53 of 1–68 days of age from Lower Quinsam, Middle Quinsam, and Comox Burn, 94% had some stones in their gizzards. Three with none were 10, 11, and 15 days of age (among 17 chicks ≤15 days of age). Our data indicate that dry mass and number of stones taken increase gradually up to ~6 weeks of age, then rise rapidly (Fig. 12.5) [4a, b].

Stones taken range from small grains of sand, ≤2 mm, to >4 mm in diameter. Size increases with age of chicks, with a sharp rise at ~6 weeks (Table 12.8). An increased mass and number and size of stones at this age may reflect an increased need for mastication, resulting from a decline in availability of seeds from fleshy fruits in late summer (see below), or a decline in the proportion of insects in the diet and their replacement by more fibrous foods. By ~70 days of age, mass of grit approaches that in older grouse (Fig. 12.5, chicks; Table 12.9, older grouse).

Only quartz, feldspar, and basalt were found in 14 gizzard samples from Comox Burn. Quartz was present in 13 and accounted for 71% of all stones (total n = 2584 stones; analysis by DC Parkyn). Feldspar was present in all samples and accounted for 28% of the stones, with basalt in three samples, 1%. Clearly, quartz dominated in these samples.

Table 12.7. Frequency of occurrence (%), mean volume (cc), and mean mass (g) of grit in crops and gizzards as reported in various studies. Sample sizes are in parentheses.

Area (season)	Frequency of occurrence	Volume[a]	Mass	Source[b]
CROPS				
ID–OR–WA (all year)		0.02 (124)		1
Vancouver Island (all year)[c]	5 (104)			2
Vancouver Island (June–October)[d]	11 (?)	t		3
Vancouver Island (March–September)[d]	13 (823)		0.11 (118)	4
Arizona (fall)	11 (99)	t		5
Northcentral Washington (fall)	23 (602)	t		6
Western Washington (fall)	26 (61)	t		7
GIZZARDS				
ID–OR–WA (all year)		6–8 (125)		1[e]
ID–OR–WA (all year)	98 (115)	7.2		8[e]
Southwestern Alberta (May–August)	98 (38)			9
Lower Quinsam (June–October)[d]	100 (20)	3.6 (20)		3[e]
Lower–Middle Quinsam (January–November)	100 (170)	3.7 (170[f,g])	9.6	10
Comox Burn (April–July)	100 (120)		8.2 (120[f])	11

[a] t, trace; reported as immeasurable or in very small quantities.

[b] 1, Beer (1943); 2, King (1971); 3, Fowle (1960); 4, King and Bendell (1982); 5, LeCount (1970); 6, Boag (1963); 7, Dragness (1968); 8, Beer and Tidyman (1942); 9, Boag (1958); 10, this study (analyses by R Snyder); 11, this study (analyses by DC Parkyn).

[c] Subalpine population.

[d] Lowland population.

[e] Beer and Tidyman (1942), and presumably Beer (1943), reported dry volumes; Fowle (1960) measured volume by water displacement.

[f] Adults and yearlings of both sexes.

[g] Includes some subalpine samples (analyses by DG King).

(b) *In yearlings and adults.* We examined dry mass and volume of grit in the gizzards of 170 adult and yearling grouse from Lower Quinsam, Middle Quinsam, and subalpine Vancouver Island (Table 12.9); all had some. Adult males had significantly more than yearling males and females in terms of both mass [5a, c] and volume [6a, c]. Differences approached significance compared to adult females [5b, 6b]. Neither mass nor volume differed among yearling males, adult females, and yearling females [7a–c and 8a–c, respectively]. Mass also varied among sex and age classes in 123 birds from Comox Burn (Table 12.9). Adult males did not differ from yearling males [9a], had less grit than adult females [9b], and more than yearling females [9c]. Yearling males did not differ from adult females [10a], and had more than yearling females [10b]. Adult and yearling females did not differ [10c].

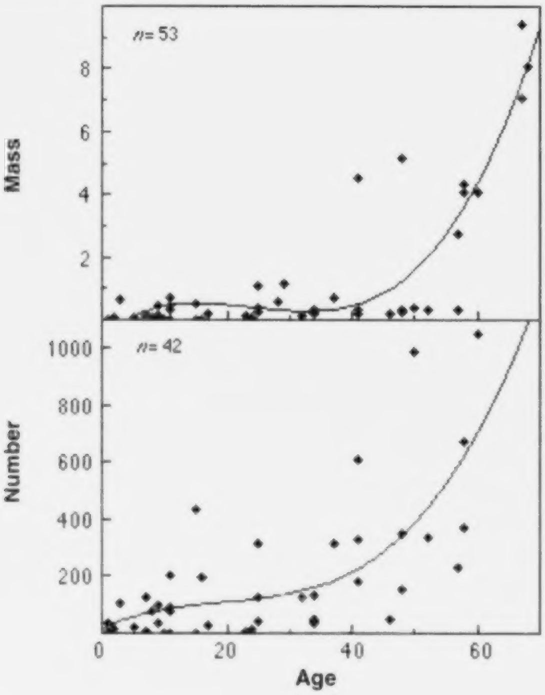
Overall, adult males tended to have more grit in terms of mass and volume than other sex and age classes, with little or no differences among the others. This may relate to the larger body size of adult males. In terms of amount relative to body size, adult males are likely not different from the others (because female body mass shows considerable seasonal variation and because of how our data were recorded and seasonally distributed, we cannot make comparisons to adult males on the basis of body mass). Adult males in this area are on nee-

Table 12.8. Number and size of stones in gizzards of chicks, by age of chicks, Comox Burn.

		Percent within each size class (mm)				
Days of age (*n*)	Mean no. of stones	<1	>1–2	>2–2.8	>2.8–4	>4
1–10 (11)	48	36	59	5	0	0
11–20 (8)	130	28	65	7	0	0
21–30 (5)	99	47	44	9	0	0
31–40 (6)	116	43	43	13	1	0
41–50 (7)	380	17	57	24	2	<1
51–60 (5)	531	25	61	13	1	0

Note: Stones sorted by DC Parkyn in stacked sieves with the following mesh sizes: 1, 2, 2.8, and 4 mm.

Fig. 12.5. Mass of grit (g), and number of stones, in gizzards of juveniles by age in days. Data from lowland Vancouver Island.



dle diets longer than females, and this might affect the amount of grit held in the gizzard. Mean volumes at Lower and Middle Quinsam were generally similar to those reported by Fowle (1960; our Table 12.7) for birds at Lower Quinsam in the early 1940s.

As in other wild galliforms (Dalke 1938; Semenov-Tyan-Shanskii 1960; Westerskov 1965; Myrberget et al. 1975; May and Braun 1973, among others), amount of grit in gizzards from Vancouver Island varied seasonally, but differed in males and females (Fig. 12.6). That in males remained fairly constant in spring and early summer, with a rise in late summer that continued into autumn [11a]. That in females indicated a significant negative trend in mass from spring to late summer [11b], but we have no data for females extending into autumn. Volume followed essentially the same seasonal patterns in both sexes [12a, b]. An increase in mass and volume in males in late summer and autumn agrees with King and Bendell's (1982) observation that frequency of occurrence in crops increased at this time. Their postulation that a rise in late summer may be a preparation for the fibrous winter diet and habitat (decreased availability due to deep snow; see 12.4.4) seems reasonable. The negative trend among females may reflect a substitution of hard seeds for grit (Beer and Tidyman 1942; and see 12.4.5(d)) or a shift to more easily digested foods, for it coincides with an increasing consumption by females of fleshy and pulpy fruits (Fig. 12.4) in the period covered by our samples.

12.4.3 Relation to body mass

Seasonal variation in amount of grit in the gizzard may vary with body mass. In males, a regression of grit mass against body mass was almost significant [13a]. The lack of significance may relate to an increased intake of grit in autumn in preparation for winter (Fig. 12.7), a time when body mass does not seem to be increasing at the same rate. In females there was a clear positive relationship between amount of grit and body mass [13b]. A general decline in body mass of females from spring to summer (Fig. 9.1) is likely the principal reason for the decline with progression of the spring and summer seasons.

12.4.4 Winter retention

Many blue grouse winter at upper elevations in areas with deep snow, where availability of small stones is restricted during much of the season. Marshall (1946) noted that gizzards of

Table 12.9. Mass (g, mean ± SE) and volume (cc, mean ± SE) of grit in gizzards of adults and yearlings from Lower and Middle Quinsam[a] and Comox Burn.[b] Sample sizes are in parentheses.

	Mass		Volume	
	Mean	Range	Mean	Range
LOWER AND MIDDLE QUINSAM				
Adult male (103)	10.2±0.30	0.1–21.9	3.9±0.11	0.1–8.4
Yearling male (30)	8.7±0.34	5.0–12.1	3.3±0.13	1.9–4.7
Adult female (21)	9.0±0.54	5.7–15.9	3.4±0.22	2.2–6.0
Yearling female (16)	8.1±0.68	3.2–13.8	3.1±0.28	1.1–5.5
COMOX BURN				
Adult male (43)	9.1±0.28	4.2–13.2		
Yearling male (19)	8.7±0.33	6.6–12.9		
Adult female (38)	9.4±1.06	3.2–13.5		
Yearling female (23)	6.9±0.34	1.9–10.2		

[a] Analyses by R Snyder. Includes some subalpine samples (analyses by DG King), which did not differ from those at Lower and Middle Quinsam.

[b] Analyses by DC Parkyn.

Fig. 12.6. Mass of grit (g) in gizzards of yearling and adult males (data combined) and yearling and adult females (data combined) by date. Data are from lowland and subalpine Vancouver Island.

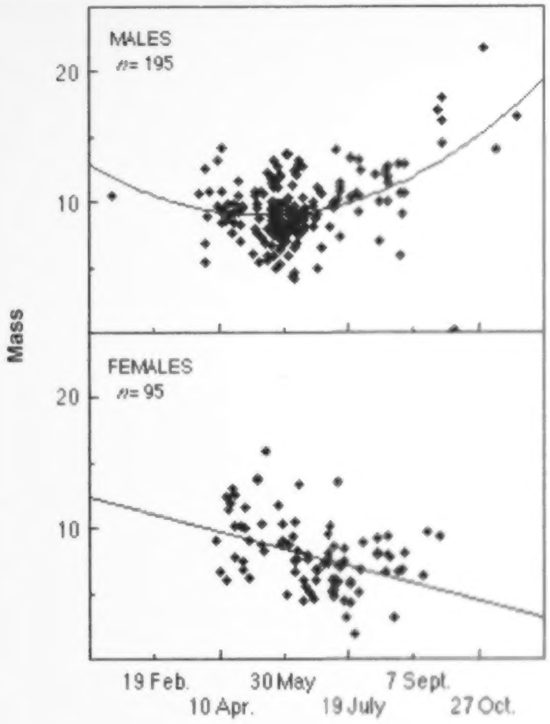
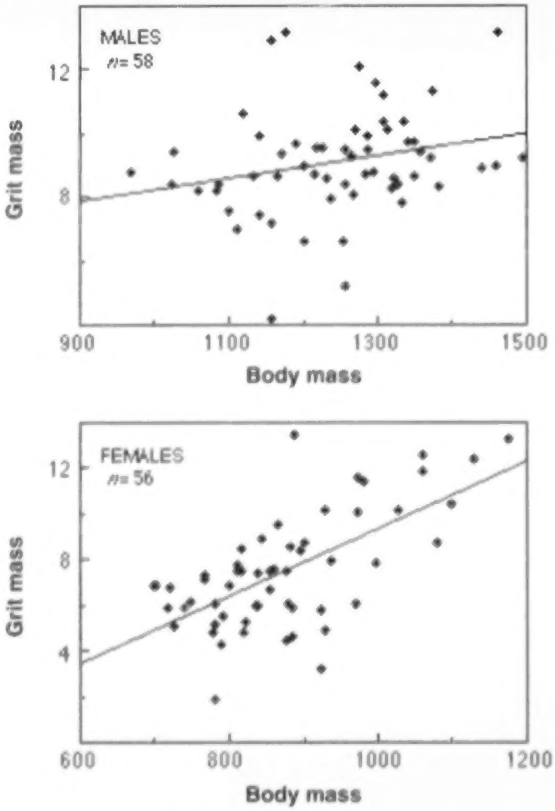


Fig. 12.7. Mass of grit (g) of yearling and adult males (data combined) and yearling and adult females (data combined) in relation to body mass, Comox Burn.



four blue grouse collected in a deep snow area in February contained as much grit as in gizzards of eight birds collected in July and August. He suggested that blue grouse retain stones in the gizzard for several months in periods of low availability, as reported, or shown experimentally, for other galliforms (Leslie and Shipley 1912; McCann 1939; Gerstell 1942; Sturkie 1965). Even in areas of deep snow, small amounts may be exposed in cavities around rocks or on the ground where a tree has fallen. We doubt that grit is a limiting factor on winter range.

12.4.5 Kinds of, and selection of, stones

Grit may vary in size, hardness, and chemical composition.

(a) *Size.* Lattner (1981) examined size of gizzard stones from 51 grouse collected in spring and early summer (presumably adults and yearlings) at Middle Quinsam. He reported a preference for stones 2.5–4.99 mm in diameter. At Comox Burn, 91% of those from adult and yearling males and 93% of those from adult and yearling females were 1–2.8 mm in diameter (Table 12.10). Differences between the two areas likely reflect availability.

(b) *Hardness.* Numerous authors have noted that quartz is the predominate mineral constituent of grit in various galliforms (Leslie and Shipley 1912; McCann 1939; Westerskov 1965; May and Braun 1973; Myrberget et al. 1975, among others). In blue grouse, Beer (1943, p. 40) reported, "Quartz was used wherever available". Boag (1958, p. 52) noted, "it [grit] was in the form of small quartz chips". At Middle Quinsam, Lattner (1981) suggested that quartz and quartzites were selected. Stones in gizzards were 4–5 times harder [reflecting a high proportion of quartz and quartzites] than samples of road gravel and forest soil. At Comox Burn, quartz occurred in all gizzards among 47 adult and yearling grouse and accounted for 84% of all stones (Table 12.11). Since quartz is very hard and relatively insoluble (McCann 1939), it is likely selected principally for grinding.

Feldspar, also relatively hard, is often reported from gizzards of tetraonines (e.g., Semenov-Tyan-Shanskii 1960; May and Braun 1973; Myrberget et al. 1975). This was the second most abundant mineral in gizzards from Comox Burn, with small amounts of basalt and serpentine, and traces of calcite and fluorite (Table 12.11). Although feldspar and basalt were taken relatively frequently, they accounted for only a small percentage of the total number of stones. Lattner (1981) also found feldspar in gizzards at Middle Quinsam, but provided no information as to its relative amount.

(c) *Mineral composition.* A considerable amount of literature has focussed on the proposal that grit may be selected in part for its mineral composition (McCann 1939; Labisky et al. 1964; Kopische 1966; Jones et al. 1968; Myrberget et al. 1975; Norris et al. 1975, among others). Most such workers have indicated that use of calcareous stones might indicate a short-

Table 12.10. Size of gizzard stones in adults and yearlings, Comox Burn.

		Percent within each size class (mm)				
Sex (*n*)	Mean no. of stones	≤1	>1–2	>2–2.8	>2.8–4	>4
Males (72)	513	2	49	42	7	<1
Females (57)	542	3	60	33	4	<1
All birds (129)	526	2	54	38	6	<1

Note: Stones sorted by DC Parkyn in stacked sieves with the following mesh sizes: 1, 2, 2.8, and 4 mm.

Table 12.11. Frequency of occurrence (%) and percentage of stones of various minerals in gizzards of adults and yearlings at Comox Burn.

	Percent					
Sex and age (*n*)	Quartz [7][a]	Feldspar [6]	Basalt [5–6]	Serpentine [4–5]	Fluorite [4]	Calcite [3]
ADULT MALE						
Freq. of occ. (18)[b]	100	83	83	28	0	11
Number (8038)	90	7	2	≤1	0	≤1
YEARLING MALE						
Freq. of occ. (11)	100	100	91	55	10	0
Number (5099)	83	12	5	≤1	≤1	0
ADULT FEMALE						
Freq. of occ. (11)	100	100	91	0	0	0
Number (5312)	81	18	2	0	0	0
YEARLING FEMALE						
Freq. of occ. (7)	100	100	86	14	0	0
Number (3543)	79	19	2	≤1	0	0
ALL BIRDS						
Freq. of occ. (47)	100	94	87	26	2	4
Number (21 992)	84	13	3	≤1	≤1	≤1

Note: Analyses by DC Parkyn.

[a] Hardness ratings (Mohs' Scale) of mineral and rock types are in brackets; higher the number, harder the stone.

[b] Sample sizes: frequency of occurrence, no. of gizzards; number, no. of stones.

age of calcium in natural foods, especially for females at time of egg formation. That calcareous stones usually occur in small quantities in most samples is often discounted by the argument that they, and other soft stones, may have been ground away by the harder components or been dissolved by stomach acids. Lattner (1981) suggested this may happen at Middle Quinsam but was unable to substantiate it. Parkyn (pers. comm.) felt that because there was little wear on stones in samples from Comox Burn, erosion of softer stones would not explain the high frequency of quartz in his samples. Thus, there is only speculation to indicate that stones may be selected for their mineral content by blue grouse. May and Braun (1973) rejected this hypothesis for white-tailed ptarmigan in Colorado, and Myrberget et al. (1975, p. 211) noted that R Moss experimentally demonstrated a selection for quartz and "... against soft stones, such as those rich in calcium" in red grouse.

(d) *Hard seeds as grit.* Hard seeds may be substituted for stones in some galliforms (Leslie and Shipley 1912; Beer and Tidyman 1942; Fowle 1960; Semenov-Tyan-Shanskii 1960; Westerskov 1965), a conjecture based on the observation that there tends to be an inverse relationship between amount of stones and that of hard seeds in the gizzard. Beer and Tidyman provided the most comprehensive review of this subject, based in large part on work with blue and ruffed grouse.

Among 115 blue grouse, Beer and Tidyman showed that the volume of stones in the gizzards varied from about 0.5 to 16 cc. Hard seeds regularly appeared at low levels when stone volume was <~12 cc and rose rapidly when it was <4–5 cc. They proposed that large quantities of seeds may displace stones. They also tested samples of seeds and stony grit for the presence of calcium, finding it in seed-coats but not in stones. From this, they suggested (p. 71) seed-coats "... may ... aid in supplying calcium".

"Substitution of hard seeds for stones" implies that seeds may be selected as a replacement. Seeds of bearberry, bunchberry, false Solomon's seal (*Smilacina* sp.), stoneseed (*Lithospermum* sp.), hawthorn, wild cherry, rose, trailing blackberry, and snowberry have been identified as possible substitutes for stones in blue grouse (Beer and Tidyman 1942; Boag 1958; Fowle 1960). Most of these plants have fleshy or pulpy fruits and may have been taken mainly for their food values, with seeds replacing, or displacing, stones in a passive rather than an active sense. This, then, is an alternative explanation to that which implies these fruits are selected for the value of their seeds in mastication. No data are available to support or reject either hypothesis.

12.5 Excretion

Virtually nothing is known about the physiology of excretion in blue grouse, but it is likely similar to that of other galliforms. Nevertheless, some clues can be derived from the examination of fecal droppings (excreta) of wild birds that contribute to our understanding of food habits, digestion, and behaviour.

Blue grouse, along with most, likely all, other tetraonines produce three principal kinds of fecal droppings, "rectal" (Sturkie 1965; "single" of Bendell 1954; "intestinal" of Zwickel 1992), "cecal", and "clocker". On well-populated ranges, these droppings are ubiquitous (Zwickel and Bendell 1985) and, with those of other organisms, contribute to the recycling of nitrogen, fibre, minerals, and other substances in the environment. Numbers and locations of droppings can also contribute to our understanding of abundance, habitat selection and other behaviours, and may be important agents for the dispersal of parasites and plant seeds.

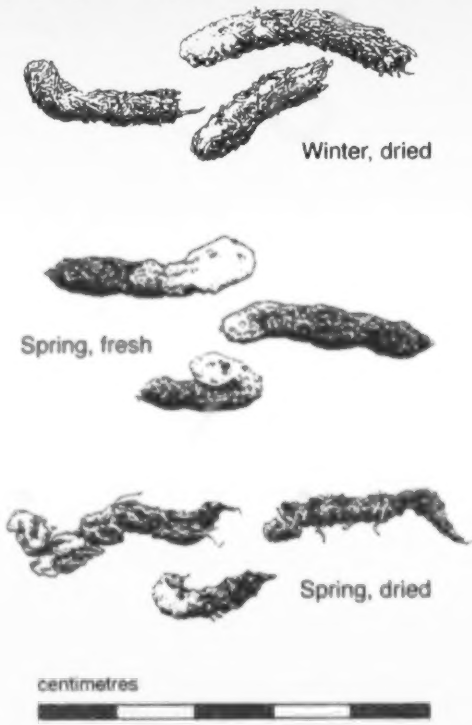
12.5.1 Rectal droppings

(a) *Form and composition.* Rectal droppings are principally fibrous, low-moisture excreta that have bypassed the ceca. Throughout most of the year they are cylindrical, about 0.5–0.75 cm in diameter, and in yearlings and adults tend to break into 2–3 cm long fragments on being voided (Fig. 12.8). Those of males tend to be larger in diameter than those of females. They are proportionally smaller in chicks, depending on age, than in yearlings and adults.

In winter, rectal feces are light greenish or brownish when first passed, turning dark brown with time since passage. They consist mainly of fibrous remnants of conifer needles, twigs, and buds. Their initial colour seems to reflect a blend of whitish twig, brownish bark, and greenish needle fragments. Some may be coated on one end with a whitish paste, presumably uric acid. Gross appearance indicates a large component of the winter diet is poorly macerated and undigestible, for woody fragments of twigs and bark comprise a principal part of the droppings. Needle fragments can sometimes be identified to species or genus. In spring and summer, when birds are taking succulent herbs and fruits, rectal droppings tend to be softer, more moist, less consistent in shape, and are often filled with intact berry or other fruit seeds. Colour, shape, and moisture content vary with kinds of foods eaten and small amounts of grit are sometimes voided in them.

(b) *Timing and locations where voided.* Rectal feces are passed throughout the day, and their locations vary with activity of the birds. They may be scattered widely, often singly, on breeding range, and one or two are often found in dust bowls, presumably voided at termination of dusting. Favourite hooting posts of territorial males can often be identified by accumulations of relatively large diameter droppings scattered over a small area, often under particular trees or on particular stumps, logs, rocks, or small heights. A single dropping is often passed by a disturbed bird just prior to, or in the act of, flushing.

Fig. 12.8. Rectal droppings in winter and spring. White on the ends of droppings is presumably uric acid. Drawings by ChW Gronau.



Concentrated piles of rectal droppings (~10 cm in diameter) on snow (Fig. 12.9) usually reflect sites of winter or early spring roosts and are often in the open, not under trees or bushes. They are often found in spring after the ground is clear of snow, now dried (Fig. 12.9). King (1971) suggested overnight snow roosts usually contain 18–24 droppings, but their number is difficult to count (or estimate) because of breakage when being passed, or by activity of the bird. What appear to be overnight roosts often contain ~30 to ~100 fecal fragments (Table 12.12). Those with >25–30 may represent more than 1 night's deposit, e.g., a day and night, or a day and 2 nights during a period of stormy weather. We have no evidence that ground roosts are used more than once, but this cannot be discounted. Rectal droppings tend to be scattered under feeding or roosting trees on winter, or early spring, range (Fig. 12.10), a reflection of the arboreal lifestyle of this bird at this time of year. Winter feeding and roosting trees, individually or in small groves, can have accumulations of droppings up to 2.5 cm deep (Marshall 1946), ≥1 bushel beneath them (Beer 1943).

(c) *Droppings as indicators of habitat selection.* We have done little winter work but have examined a number of winter ranges in summer. Accumulations of winter droppings indicate a strong selection for certain trees for feeding or roosting, as suggested by others (Beer 1943; Wing 1947; King 1971; Zwickel and Bendell 1986; Cade and Hoffman 1990). Two examples from our notes illustrate this point:

Fig. 12.9. Droppings in, or from, snow roosts: *top*, fresh rectal droppings, upper, and to their lower right, a fresh cecal dropping; *bottom*, dried rectal droppings in spring.

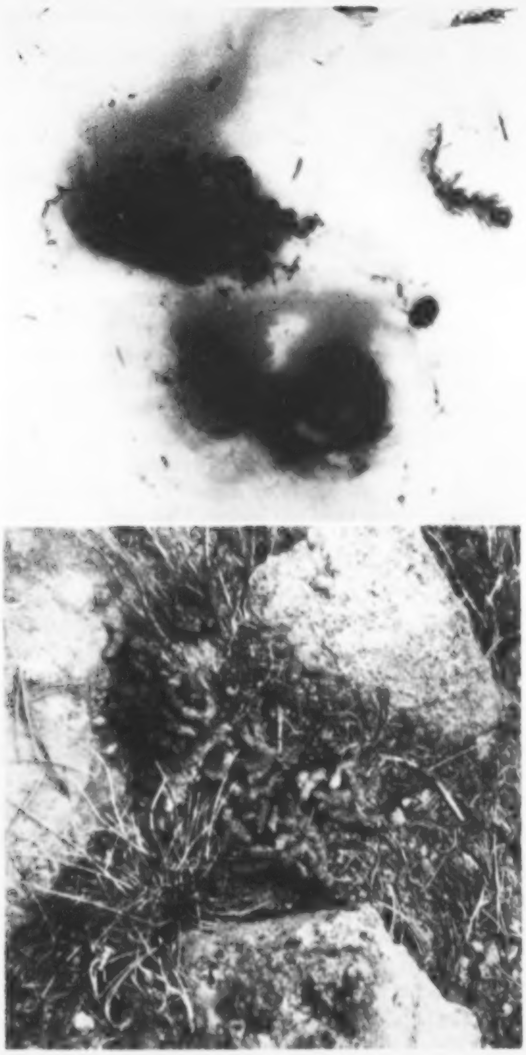


Fig. 12.10. Rectal droppings under a spring feeding tree, Hart's Pass, WA, 2 May 1961.

Snow Basin near Ogden, UT, 19 June 1978—in a grove of mixed conifers we counted or estimated numbers of winter droppings under all trees in this grove: 21 Douglas-firs, 11 subalpine firs, and 1 white fir. Douglas-firs ranged in height from ~4 to 20 m (16/21 ≥10 m); subalpine firs, ~4 to 10 m (8/11 ≤5 m), and the white fir was ~15 m tall. Droppings were found under eight Douglas-firs, two subalpine firs, and the white fir. Numbers under Douglas-firs ranged from 2 to ≥500 (7/8 had ≥10), while only one was found under each of the other species.

Douglas Creek, Medicine Bow National Forest, WY, 1 July 1978—on a ridge with scattered Douglas-fir along the crest and more or less solid lodgepole pine forest on the north-facing slope, just below the crest. All Douglas-firs had some droppings under them, 10–15, up to 100–200. About 50% of large lodgepole pines had a few, rarely >10.

Droppings were a clear indication of selection in these cases, but we cannot say with certainty that it was only for particular species of trees; e.g., at Snow Basin, it may have been partly related to size of trees and at Douglas Creek, location of trees. However, in both cases, Douglas-fir was most used, consistent with suggestions this is a preferred food species (Beer 1943; Zwickel and Bendell 1986; Remington 1990).

Table 12.12. Numbers of rectal droppings in fresh snow roosts at Tsolum Main.

Date	Depth of snow (m)[a]	No. of droppings[b]	Overhead cover
13 April 1974	1.2	28	~10 m to nearest tree or bush
7 April 1975	0.8	100	1.8 m Douglas-fir
1 April 1974	1.2	30	6 m amabilis fir
13 April 1975	1.1	75[c]	Inside fir–hemlock thicket
16 April 1975	0.6	100[d]	2.4 m Douglas-fir
7 April 1976	0.6	50	~1 m to edge of nearest tree

[a] Depth of snow is approximate for the area in the immediate vicinity of the roost during spring thaw, and on broken ground depths may vary greatly over short distances.

[b] Numbers of droppings are approximate; see 12.5.1(b) for problems in counting or estimating numbers.

[c] Fresh cecal dropping about 3 m from roost, on top of snow.

[d] Fresh cecal dropping reported here but exact location not recorded.

12.5.2 Cecal droppings

Cecal droppings, as their name implies, are produced in the ceca. On being voided they are usually single, amorphous, greenish brown, and loosely pasty. On exposure to drying they quickly develop a dark brown "skin". Fresh cecal droppings are most often found in early morning, are often associated with night roosts, and most commonly appear to be passed at, or shortly after, termination of roosting, often on top of, or adjacent to, a pile of rectal droppings (Fig. 12.9). If voided from the ground, a single cecal dropping may cover an area ≥9 cm^2 and be 3–4 mm thick; if from a tree, they may splatter over a larger area. They have a strong odour that is readily detected by dogs and, if very fresh, even by humans. Smaller cecal droppings are sometimes voided at other times of day, but numbers are much fewer relative to rectal droppings.

12.5.3 Clocker droppings

Clocker droppings ("clockers", of Leslie and Shipley 1912) are passed only by hens and are comprised of a coil of rectal droppings (Fig. 12.11) that accumulate in the rectum while the hen is incubating eggs or overnight brooding of very small chicks (Zwickel 1967*a*). Bendell (1954, p. 75) described clockers as ". . . up to 10 times the size of a single scat and wound as the coils of an elongated spring." One end is usually coated with a whitish paste, presumably uric acid. This may reflect a high nitrogen diet of the incubating hen.

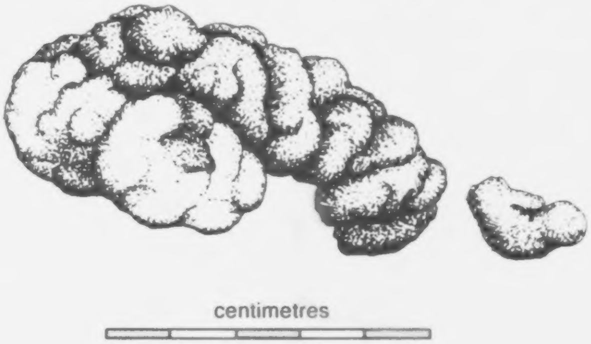
Clockers are often voided by incubating hens at feeding sites (Bendell 1954), after an extended bout of incubation. The hen may walk or fly to the site before voiding, sometimes at some distance from the nest. At Lower Quinsam, clockers were concentrated in open cover types and led Bendell (1954) to conclude these were important feeding areas for nest hens. One is occasionally left in, or near, the nest at time of final departure of the hen and brood.

12.6 Synthesis

Owing to the broad range of habitats in which blue grouse are found, species of foods taken vary widely. Nevertheless, selection undoubtedly occurs among species, higher taxa, and parts of plants eaten.

This grouse is primarily a vegetarian throughout the year, although chicks take many invertebrates in their first weeks of life, presumably to obtain protein for growth and development. Spring and summer diets are mainly comprised of leaves, flowers, seeds, and fruits of herbaceous plants and low-growing shrubs and are constantly changing in terms of species composition, as availability changes. Despite that generalization, birds in some populations, especially males, eat significant amounts of conifer needles in spring. Winter diets are mainly comprised of needles, buds, and twigs of coniferous trees. Blue grouse are one of few species of vertebrates that exist almost solely on conifers in winter, a fundamental feature of this bird. Aviary studies indicate conifers can supply daily nutritional and energetic requirements and should not be considered a low-quality food for this species.

Fig. 12.11. Clocker dropping of an incubating female. White on the large end is presumably uric acid. Drawing by ChW Gronau.



In spring, hens shift earlier than males to herbaceous foods, presumably to fulfill requirements for laying eggs, incubation, and subsequent care of chicks. Many species or groups of invertebrates have been identified as foods of blue grouse, especially for young chicks. Food selection has been clearly documented in blue grouse. Nutritional quality and (or) toxic chemical composition of plants have been proposed as principal reasons for selection or avoidance of individual species. But, there are no clear answers to these hypotheses because most studies have not included bioassays with grouse. More work is needed in this area.

Water, as an essential component of the animal body, is usually ingested as free water or as a component of food. Most evidence suggests wild grouse obtain sufficient water from their food. Nevertheless, they may be excluded from very zeric habitats by lack of water or sufficiently succulent foods, but this is speculative.

Small stones are used in the mastication of food in the gizzards of virtually all tetraonines. Amount of grit varies seasonally, more in spring, less in summer. This parallels seasonal differences in fibre content of the diet; more fibre equals more grit. Quartz and feldspar are the principal mineral constituents of stones taken by blue grouse. They are very hard, relatively insoluble, and are likely selected principally for mastication. We have little evidence to support the suggestion that kinds of grit are selected in part for their nutritional (mineral) contents.

Blue grouse excreta are comprised of three distinct kinds of fecal droppings—rectal, cecal, and clocker. Rectal and clocker droppings have been used to examine food habits and various aspects of behaviour and to make inferences about digestion.

Overall, with respect to food, water, and grit, blue grouse seem well adapted to occupy the many different habitats in which they are found. Except for their seeming dependence on conifers in winter, they are truly generalists in these respects.

Endnotes [Chapter 12]

1. King (1968) found a maximum of 9.2 g dry mass in an adult male crop from Vancouver Island (*n* = 820 crop samples analysed). At 80% moisture content this would represent ~58 g wet mass.

2. Nocturnal feeding has not been documented, but this may reflect the habits of biologists rather than those of grouse.

3. Observations of seven chicks under ~2 weeks of age showed that in 492 feeding pecks, ~10% were at the ground, the rest at upper

and lower surfaces of leaves. Among 1063 pecks of three 2–4-week-old chicks, ~30% were at the ground, significantly more than by the younger birds [1]. Small chicks appeared to be taking small insects, e.g., aphids and ants, from vegetation but took larger, ground-dwelling forms as they grew older.

4. Beer analysed 128 crop and gizzard samples from birds collected year round in Idaho, Oregon, and Washington. Stewart examined 288 year-round crop samples from various parts of the range of blue grouse. Beer and Stewart considered adults (includes yearlings) separate from juveniles but did not separate either by sex. Standing examined 100 spring and summer crop samples from the Methow Valley. He combined data for sex and age classes but appears to have sampled only adults and yearlings. King analysed 125 spring, summer, and autumn crop samples from subalpine Vancouver Island; he separated data for adults (includes yearlings) by sex, but not juveniles. Schladweiler, examined 566 spring, summer, and autumn crop samples from various areas in Montana (80% from autumn); he separated data for adults (includes yearlings) by sex, but not juveniles, in his spring and summer samples but combined all sex and age classes in autumn analyses. (He reported data only for plants that comprised 5% by volume.) King and Bendell analysed 811 spring and summer crop samples from early forest seres on Vancouver Island; they separated data for adults (includes yearlings) by sex but not for juveniles. In all such studies, including dropping analyses, different foods may be more thoroughtly digested than others or pass through different sections of the gastrointestinal tract at different rates.

5. Requirements of tetraonines are sometimes surmised on the basis of those of near-relatives, most often domestic poultry (e.g., Stiven 1961; Moss 1967; Savory 1977; Beckerton and Middleton 1982; King and Bendell 1982). This may not be valid.

6. An alternative explanation might be that ruffed grouse from Vancouver Island require more water than those in New York.

7. Grit increases the digestibility of whole grains and seeds in domestic poultry by ~10% (Sturkie 1965).

CHAPTER 13

Energetics

> *Maintenance energy expenditure is . . . the necessary chemical energy ingested to maintain basic body functioning or basal metabolism, to support activity costs, and to thermoregulate by balancing heat loss with heat production.*
>
> CT Robbins (1983)

Little direct research has been done on energetics in blue grouse and much of what is known, or suspected, is based on circumstantial evidence. Some information is available on the development of homeothermy (see 11.4), body temperature, metabolic rates, lower critical temperatures, energy requirements, metabolizable energy, and behaviour as related to winter energetics.

13.1 Body temperature

13.1.1 Grouse on Vancouver Island

Few data are available on body temperatures (t_bs) of most species of grouse, and only one report has been published for wild blue grouse (Zwickel 1992). We expand here on that report for birds from Vancouver Island.[1]

(a) *Yearlings and adults.* We found no difference in mean t_bs between yearling ($n = 19$) and adult ($n = 42$) males [1a], with an overall mean of 42.0 ± 0.07°C. A mean of 41.9 ± 0.11°C for yearling females ($n = 22$) was significantly lower than the 42.3 ± 0.09°C of adults ($n = 37$) [1b], with an overall mean of 42.1 ± 0.08°C. Most yearling females for which t_b was measured were broodless (20/22), while most adults had broods (25/34), indicating that brood hens might have elevated t_bs. However, within adults, there was no difference between brood ($n = 25$) and broodless ($n = 9$) females [1c]. The sample of yearlings with broods was too small for a similar comparison.

Small birds tend to have higher t_bs than larger birds (Sturkie 1965), but the lower t_b of yearling than adult females contradicts this generalization. Nevertheless, within age classes, there was a significant inverse relationship between t_b and body mass in both age classes (Fig. 13.1) [2a, b], in agreement with Sturkie's suggestion. These analyses indicate a positive relationship between mean t_b and mean body mass of yearling and adult females, but a negative relationship within age classes.[3] No such relationships were detected in males [3].

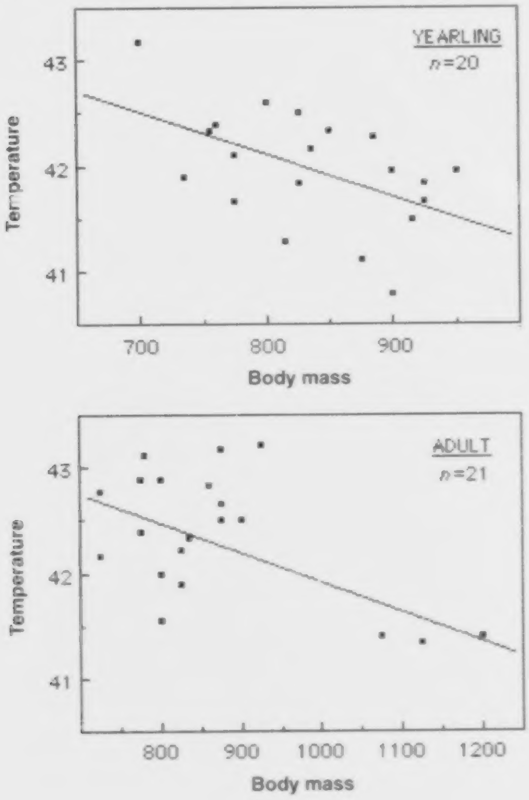
(b) *Juveniles.* We measured no t_bs of very young grouse (≤10 days of age), but have those of 12 chicks between 35 and 67 days of age. Their mean t_b was 41.8°C, not different from the overall mean of 42.1°C of yearlings and adults. Others, however, have reported lower temperatures in small chicks than older birds in other grouse. Robinson (1980) and Myhre et al. (1975) found that t_b increased with age in young spruce grouse and willow ptarmigan. That of 3-week-old spruce grouse was about 1.7° less, and of 1-day-old willow ptarmigan about 1.3° less, than in adults. Body temperatures of newly hatched hazel grouse, 38.1°C (Bergman et al. 1978), and young black grouse, 39.3°C (Rintamaki et al. 1983), were ~2° lower than in adults. Newly hatched capercaillie, at 37.9°C, attained adult temperature, 41.6°C, on day 18 (Hoglund and Borg 1955, cited in Welty 1964, not seen by us). A difference can be expected between very young chicks and older blue grouse.

13.1.2 Comparison to other species

Body temperatures of yearling and adult males combined did not differ from those of yearling and adult females combined [1d], with a grand mean of 42.1 ± 0.05°C (40.3–43.3°C). This compares to means of 40.3– 43.5°C reported for 11 other species of birds[2] from six orders—Pelecaniformes to Passeriformes (Sturkie 1965). Mean t_b of the domestic chicken, the nearest relative to blue grouse within Sturkie's sample, was 41.9°C, very close to that of our species. Mean t_bs reported for other adult tetraonines are as follows: ruffed grouse, 42.1°C (Long 1947); spruce grouse, 41.9°C (Robinson 1980); hazel grouse, 40–41°C (Bergmann et al. 1978); black grouse, 41.6°C in summer and 40.3°C in winter (Rintamaki et al. 1983); capercaillie, 41.6°C (Hoglund and Borg 1955, cited in Welty 1964); and willow ptarmigan, 40.7°C (Myhre et al. 1975). Our mean for blue grouse was identical, or very similar, to those of ruffed and spruce grouse, but slightly higher than those of hazel grouse, black grouse, capercaillie, and willow ptarmigan.

To the best of our knowledge, only Pekins (1988) has documented t_bs for blue grouse outside of Vancouver Island. He reported a mean of 39.5°C (38.4–40.2°C) for three *D.o. obscurus* males in captivity, lower than our data suggest for wild *D.o. fuliginosus*. His t_bs were taken during wind-speed metabolism experiments at −15°C and may represent subnormal values for the species. Alternatively, winter t_bs may be lower than in summer, when ours were taken. Pekins noted that the lowest t_b did not occur at the strongest wind and suggested his birds could thermoregulate at all environmental conditions to which they were subjected.

Fig. 13.1. Body temperatures (°C) of yearling and adult females regressed on body mass (g), Vancouver Island.



13.2 Metabolic rates and lower critical temperatures

13.2.1 Metabolic rate

Pekins et al. (1992) investigated metabolic rates of *D.o. obscurus* in Utah. They reported standard metabolic rates (SMRs) of 0.812 L $O_2 \cdot (kg^{0.734}) \cdot h^{-1}$ in winter and 0.751 L $O_2 \cdot (kg^{0.734}) \cdot h^{-1}$ in summer (PJ Pekins, pers. comm.). A lower summer than winter SMR also has been reported for black grouse (Rintamaki et al. 1983) but is opposite to reports for willow and rock ptarmigan (Mortensen and Blix 1986) and capercaillie (review by Rintamaki et al. 1983).

13.2.2 Lower critical temperture (LCT)

In winter aviary trials, LCTs of blue grouse were between -5 and -10°C (PJ Pekins, pers. comm.). This is lower than comparable values reported for ruffed grouse, -0.3°C (Rasmussen and Brander 1973) and 1.5°C (Thompson and Fritzell 1988); rock ptarmigan, -1.3°C (West 1972); and black grouse, 5.5°C (Rintamaki et al. 1983); but similar to that of willow ptarmigan, -6.3°C (West 1972). Pekins concluded that high thermoregulatory abilities adapt blue grouse well for winter conditions. The summer LCT of blue grouse was between 5 and 10°C (Pekins 1988).

13.3 Energy requirements

13.3.1 Juveniles

Stiven (1961) estimated daily energy requirements for 1–4-week-old chicks with the factorial method (Maynard and Loosli 1956). Estimates were 14.1, 27.5, 53.1, and 91.1 kcal/day, at each week of age, respectively. Invertebrate foods were estimated to yield 0.91 kcal/g, plant foods, 0.57 kcal/g.[4] On the basis of these data, chicks on an invertebrate-only diet would have to consume ~15, 30, 58, and 100 g/day at each week of age, respectively, to satisfy their energy requirements. On a plant-only diet they would have to consume ~25, 48, 93, and 160 g/day at each week of age, respectively. There are no data on summer energy requirements of yearlings and adults.

13.3.2 Winter

After factoring in microclimatic data, Pekins (1988) estimated winter energy requirements of captive grouse as 138.9 kcal (581 kJ)/day, 1.34 times the caloric equivalent of the SMR (103.6 kcal (433.5 kJ)/day) and ~15% less than provided by an average daily diet of Douglas-fir needles (153.3 kcal (641.4 kJ); Remington 1986). In theory then, Douglas-fir needles can provide a positive energy balance in winter. Pekins then measured the caloric equivalent of the field metabolic rate (FMR) of seven wild males (mean mass = 1131 g) with doubly labelled water. This gave an average of 157 kcal (657 kJ)/day, 1.4 times the SMR, and 1.6 times the basal metabolic rate (BMR); within 2% of that provided by an average daily diet of Douglas-fir.

The SMR and BMR of blue grouse are normal, but the FMR:BMR ratio, 1.6, is low compared to the average of 2–3 for birds and small mammals in general. Average energy costs other than BMR (and SMR) of other birds and small mammals are almost 1.6 times higher than for blue grouse (Pekins 1988). These data indicate that winter energy costs of free-living blue grouse are less than in small mammals and many other birds. Pekins proposed that behavioural and physiological adaptations allow blue grouse to minimize energy costs.

13.4 Metabolizable energy

Boag and Kiceniuk (1968) reported a caloric content of 4.97 kcal/g dry mass in lodgepole pine needles from southwestern Alberta, similar to that reported for other species of pine (~5 kcal/g). They suggested this was high, but the percentage that could be utilized was unknown. More recently, the caloric availability of some conifer needles to blue grouse has been estimated. Remington (1990), working with captive birds, found that the metabolizable energy of Douglas-fir needles, at 1.75 kcal/g dry matter, did not differ significantly from that of lodgepole pine needles, 1.69 kcal/g. Both were greater than in subalpine fir, 1.51 kcal/g, and Engelmann spruce, 1.12 kcal/g. If most pines contain about 5 kcal/g dry mass, only about 35% of their gross caloric content is useable by blue grouse, as judged from Remington's results. This appears adequate, however, since the caloric equivalent of the winter FMR is within ~2% of that provided by an average daily diet of Douglas-fir (see 13.3.2).

13.5 Behaviour and winter energetics

Pekins (1988) also investigated behavioural traits that might be used to compensate for low winter temperatures. He proposed that subalpine firs are used selectively for night roosts because of a favourable microclimate, Douglas-firs during the day because they provide food, exposure to solar radiation, and protection from wind. He suggested (p. 70), ". . . a blue grouse would realize a 50% greater reduction in convective heat loss and a 10% greater net energy savings by roosting overnight in a subalpine fir rather than a Douglas-fir."

Diurnal and nocturnal roost sites were usually located in the lower two-thirds of the crown, close to the trunks (Pekins 1988). Nocturnal roosts had greater canopy cover than those used during the day and were more often close to the trunk. A 63% reduction in wind speed at diurnal roosts, and 85% at nocturnal roosts, was considered the primary energetic advantage of such sites. In winter, 71% (116/163) of grouse observed on sunny days were classified as sunbathing. Snow roosting (burrowing in snow) appeared less common than in other northern grouse, perhaps because of the efficient thermoregulatory abilities of blue grouse. Pekins concluded that there appears to be little energetic constraint on this bird in suitable winter habitat (see also 15.4.2).

13.6 Synthesis

Mean t_b of mature blue grouse on Vancouver Island, at 42.1°C, is generally similar to that of the domestic chicken, ruffed grouse, and spruce grouse. Mean t_bs of yearling and adult males did not differ, but that of adult females was higher than in yearling females, for which we have no explanation. We have no information on t_bs of very young chicks, but judging from information on other species of grouse, it is likely 1–2° lower than in mature birds.

Standard metabolic rates of blue grouse in winter are slightly higher than in summer according to aviary studies in Utah. Work there also indicated that lower critical temperatures are between −5 and −10°C, lower than in summer, and than reported for several other tetraonines. Caloric requirements in winter appear to be readily satisfied by the normal daily ration of Douglas-fir, a principal winter food of this species. These studies, collectively, indicate blue grouse are well adapted to survive winter conditions that are sometimes considered harsh, on foods considered by some as poor in quality. Along with the above, blue grouse exhibit behaviours that conserve energy in winter, e.g., selective use of protective roost sites.

Endnotes [Chapter 13]

1. Temperatures were measured with mercury thermometers inserted ~2.5 cm into the rectum of birds captured for banding.

2. Counting the domestic duck (genus?), goose (genus?), turkey (*Meleagris* sp.), pigeon (*Columba* sp.), and chicken as species.

3. Body temperature may vary among and within individuals of the same species according to age, size, sex, activity, food, diurnal and seasonal rhythms, t_a, plumage (including state of moult), and nesting habits (Sturkie 1965). In newly hatched willow ptarmigan, t_b may decrease during feeding and return to normal when brooding (Pedersen and Steen 1979). In older ptarmigan, it may be higher in submissive than dominant individuals following hierarchical interactions (Myhre et al. 1981). In view of the number of factors that can affect t_b, including numerous permutations, it would be difficult to identify causes of variation with certainty without controlled experiments and large samples.

4. See also 11.1.2(b) for information on residual yolk in chicks, likely an important source of energy in the first days of life.

CHAPTER 14

Genetics

> *Variation among individuals . . . may be either genetically based or environmentally induced.*
>
> CJ Krebs (1972)

Genetic variation among or within populations is ubiquitous and may be expressed at different levels, e.g., at subspecies, local population, or individual levels, and itself, may be environmentally induced. Genotypic variation may influence virtually all aspects of an individual or population's attributes and is potentially important to most fields of biology.

There has been little direct genetic study of blue grouse. Nevertheless, on the basis of work with other organisms, much research with blue grouse undoubtedly has genetic implications. The first direct genetic studies with this species were by Redfield (1972) and involved population processes. Recent phylogenetic and systematic molecular studies (Ellsworth et al. 1995, 1966; Gutierrez et al. 2000; Lucchini et al. 2001; Drovetski 2002, 2003)) also involved this bird. We review some of the principal aspects of these works here.

14.1 The *Ng* locus, a genetic polymorphism

14.1.1 Discovery of the Ng locus

Birdsall et al. (1970) first reported a new genetic polymorphism in blue grouse (and deer mice (*Peromyscus maniculatus*)), white bands on starch gels stained for esterase activity. Phenotypic frequencies of these bands were in close agreement with expected frequencies in a three-allele, one-locus genetic system and the authors named the locus *Ng*. Nature of the substance causing the bands was unknown and the authors recognized more work was needed to define its chemical origin and biological significance. Redfield (1972) considered this system potentially useful as a genetic marker.

14.1.2 Geographic distribution and temporal variation at the Ng locus

Geographic distribution and temporal variation of the *Ng* alleles and their associated genotypes were examined by Redfield et al. (1972) for several populations of blue grouse on Vancouver Island and nearby mainland British Columbia. Bands (alleles) were designated *NgS*, *NgM*, and *NgF*, for the slowest, intermediate, and fastest, respectively. Homozygotes had one band, heterozygotes two. The *NgM* band was always most common, with a frequency near 0.8 in most populations (Redfield 1973*b*), and the *NgF* band least common. Frequencies of each were generally similar over nine areas and 14 samples (multi-year samples from two areas), with no indication of clinal variation. Eleven samples were in good agreement with Hardy–Weinberg expectations, and there was no annual deviation from expectations at the areas with multi-year samples. All individuals had at least one, none more than two, white band(s), and plasma from the same bird at different times produced the same pattern. A principle conclusion was that this polymorphism is balanced and maintained by selection. Redfield and his colleagues produced other papers dealing with genetic–demographic relations in blue grouse, using the *Ng* locus as a marker—to be considered in a future publication.

14.2 Phylogeny and systematics of grouse based on mitochondrial DNA

With the advent of molecular DNA research and recent technological advances, studies of avian systematics and evolution have burgeoned, including recent studies with the tetraonines.

14.2.1 Phylogeny and systematics of North American tetraonines: relationships of blue grouse to other tetraonines

Ellsworth et al. (1995) used mitochondrial DNA (mtDNA) to examine phylogenies among North American grouse and ptarmigan. From their work, they partitioned the tetraonids into three primary groups, with blue grouse in one that included all ptarmigan and capercaillie. Spruce grouse clustered with ruffed and sage-grouse,[1] and the two prairie-chickens and sharp-tailed grouse constituted the third group. The authors suggested blue and spruce grouse have had separate evolutionary histories and do not constitute a monophyletic lineage.

Ellsworth et al. (1996) also studied the systematics of North American grouse and ptarmigan, as determined by sequencing of the cytochrome-*b* gene. Blue and spruce grouse showed the second greatest intrageneric divergence (11.45%) when compared to other congeneric species. Evolutionary relationships included a well-supported clade containing blue grouse, the two prairie-chickens, and sharp-tailed grouse. These were associated with a sister clade containing the three ptarmigan and capercaillie. Although results from this and the earlier study (1995) differed in some respects, both suggested blue and spruce grouse are not closely related within the tetraonines, leading the authors to question the supposed congeneric status of these species at that time. Their studies plus arguments by Yamashina (1939) and Dickerman and Gustafson (1996) were instrumental in the decision of the American Orntihologists' Union (AOU 1997) to remove spruce grouse from *Dendragapus* and place them in the genus *Falcipennis* (AOU 1997). See also 5.2.3(i).

14.2.2 Multi-gene sequencing and the classification of tetraonines: where do blue grouse belong?

Gutierrez et al. (2000) sequenced five mitochondrial genes—cytochrome-*b*, cytochrome oxidase-3, adenosine triphosphatase-8, adenosine triphosphatase-6, and NADH dehydrogenase-2—for all species-level taxa of grouse. The authors considered the dusky blue (their *D. obscurus*), sooty blue (their *D. fuliginosis*), spruce (their *Canachites canadensis*), and Franklin's grouse (their *Canachites franklinii*) as separate species, arguing that within each of the two generic complexes [*Dendragpus* and *Canachites*] they are as separable as the two capercaillies, two black grouse, and two hazel hens. Results of this study strongly supported the monophyly of a clade consisting of all grouse. In their classification, a clade consisting of the two prairie-chickens and sharp-tailed grouse was sister to one including the dusky and sooty blue grouse. *Dendragpus* then clustered with a clade containing sage-grouse.[1] These five species were placed in a new subtribe, Centrocercina, with the spruce and Franklin's grouse in a separate subtribe, Canachitina. Members in each of the dusky–sooty blue grouse pair and spruce–Franklin's grouse pair differed from each other by more than that between the two prairie-chickens and sharp-tailed grouse, consistent with the presumption of specific status for them. These suggestions for taxonomic changes have not yet been accepted by the American Ornithologists' Union. Most recently, on the basis of molecular and historical biogeographic analyses, Drovetski (2003) has suggested that blue grouse are a prairie grouse, most closely related to *Tympanuchus* and *Centrocercus*.

14.3 Synthesis

Direct genetic studies of blue grouse are in their infancy. The first, by Birdsall et al. (1970), identified a new genetic polymorphism, the *Ng* locus, that appears geographically and temporally stable. It has been used as a marker for demographic research, even though its biological function is unknown.

Although results of the phylogenetic and systematic studies of Ellsworth et al. (1995, 1996) with North American grouse were not completely consistent, both suggested a close relationship of blue grouse with *Tympanuchus* spp. and a distant relationship with spruce grouse. With stronger and more comprehensive molecular data, and from all grouse, Gutierrez et al. (2000) confirmed these relationships. Neither Potapov (1985) nor Boag and Schroeder (1992) agreed with the congeric status of blue and spruce grouse that was formalized in the sixth edition of the *Checklist of North American Birds* (AOU 1983). Results of the molecular studies of Ellsworth et al. and Gutierrez et al. support the view of Potapov and Boag and Schroeder. Results of molecular studies to date clearly place blue and spruce grouse in separate genera.

We once suggested that blue and sage-grouse are more alike than either is to any other species (Bendell and Zwickel 1984). We also suggested (5.2.3) that blue and sage-grouse are more closely related than blue and spruce grouse. The molecular data of Gutierrez et al. (2000) support that suggestion but indicate that blue grouse might be more closely related to the prairie-chickens and sharp-tailed grouse than to sage-grouse. In either case, more recent molecular data, including that of Lucchini et al. (2001) and Drovetski (2002, 2003), indicate a closer relationship of blue grouse with prairie species than with the spruce or other forest grouse. Blue grouse likely evolved from a prairie or prairie–forest edge ancestor and moved into forest secondarily.

Endnote [Chapter 14]

1. Now recognized as two species, the greater (*C. urophasianus*) and Gunnison (*C. minimus*) sage-grouse. No samples from the latter were included in this study.

Part 4

Behaviour

CHAPTER 15

Behaviour *per se*

> *Organisms must not be thought of as fighting against their harsh environment;*
> *they have evolved with it and their behaviour is adapted to it.*
>
> MA Lewis and LR Taylor (1967)

Our behavioural work has been directed toward describing or explaining specific behaviours or behavioural patterns. Emphasis here is on field studies but includes observations of aviary birds if helpful in eliciting or confirming actions of wild birds. Behaviour is of great importance to those involved in studies of natural history, evolution, ecology, sociobiology, and populations, among others.

It is not always possible to separate "behaviour *per se*" (actions of individuals) from results of the behaviour (e.g., use of space and habitat), and we sometimes have made choices as to where best to consider a topic.[1] Use of habitat, migration (including migratory behaviour), dispersal and site fidelity, and home ranges are considered in Chaps. 16 and 17.

Many behaviours are sex or age specific, but some are more general and apply to virtually all sex and age classes.[2] We first consider those that are general, then those that apply to males, females, or juveniles. Most behaviours described here are from our studies with *D.o. fuliginosus* in British Columbia. Although we have not seen many clear differences among subspecies, except where noted, more thorough comparative study is needed, especially with females.

15.1 General behaviours

15.1.1 Basic postures

Birds we encounter in the field are often aware of our presence when first seen. However, in at least some populations, many soon return to normal (undisturbed) activities. Unless noted otherwise, our descriptions are based on what we believe to be normal for the behaviours under consideration.

(a) *Neutral, resting, roosting, and sleeping postures.* Undisturbed grouse not involved in a specific activity are usually in a neutral posture, a standing position. The head and neck are up, and, along with the body and tail, form a more or less straight line running approximately 45° from horizontal (Fig. 15.1). The plumage is relaxed and held smoothly against the body, with no obvious alterations of body parts or feathers that reflect overt reactions to external stimuli. Birds may walk in this posture, moving at a steady, relatively slow pace, and the tail may be raised somewhat toward the horizontal. They rest, roost, and sleep in essentially this posture except that the head and neck are drawn down toward the shoulders and the legs are more bent, so the bird may appear to be sitting on its feet (Fig. 15.2). Contour feathers may be more fluffed, perhaps to provide more insulation in this relatively inactive state. Once settled for the night, birds may be found at the same location at dawn. In sleeping, the head may be turned back on the wing and the eyelids closed.

On large coastal clear-cuts, grouse often roost on the ground, as evidenced by piles of rectal droppings and radio-marked birds found on the ground well after dark. We suspect this is also true for those on shrub-steppe breeding ranges without access to trees within their home ranges. Where suitable trees are available, birds often fly into them in late crepuscular hours (Blackford 1963; pers. observ.) although Popper et al. (1996) found radio-marked grouse roosting on the ground at night, even when trees were available. Snow roosts may be used in winter (Caswell 1954*b*; King 1971), but Pekins (1988) suggests this is less common than roosting in trees, and we agree (see also 15.4.2).

(b) *Alert posture.* In typical alert posture (Fig. 15.3) the bird is clearly vigilant in response to an intrusion or disturbance. It represents an arousal in which the bird is seeking information and may reflect curiosity, alarm, and (or) aggression. Contour plumage is sleeked and the tail is often elevated, more often in males than females, but not fanned. The neck is stretched upward and slightly forward, the crest may be raised, the combs may enlarge slightly, and the legs are more straight than in neutral posture, making the bird appear tall. The bird may be motionless, or if moving (Fig. 5*a* in Bendell and Elliott 1967), the walk may be very slow, suggesting curiosity, caution, or ambivalence, faster if moving away and suggesting alarm. McNicholl (1978) described three common variants: Alert, Tail Down; Alert, Crest Down; and Partial Alert (crest and tail down). Less commonly, any of the above may be accompanied by exposure of a white shoulder spot (see 15.2.3), and of the lateral cervical apteria (males only). Variants reflect different levels of excitement and (or) temperaments of different individuals. Observer-induced growls of males (15.2.1) or clucking of females (15.3) are often given by alert birds. Such birds hold their position or move away and do not approach an observer.

Fig. 15.1. Neutral posture.

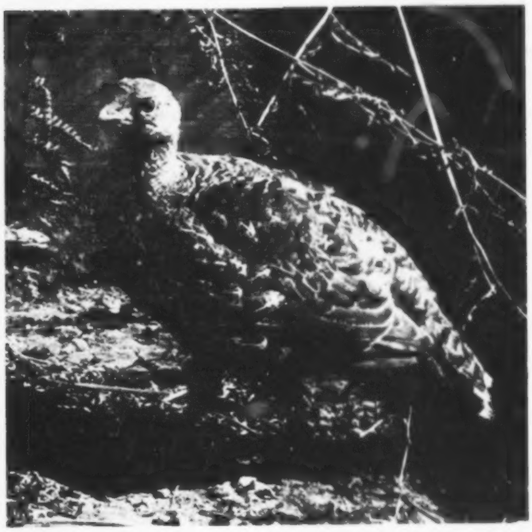


Fig. 15.2. Roosting, sleeping, posture. Drawing by ChW Gronau.

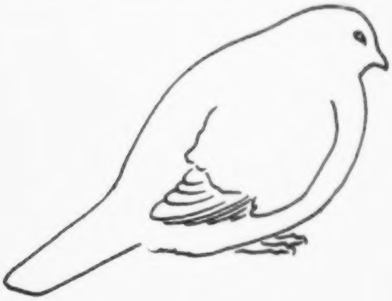


Fig. 15.3. Alert posture. Note that the bird's tail and crest are partly raised and neck is stretched upward.

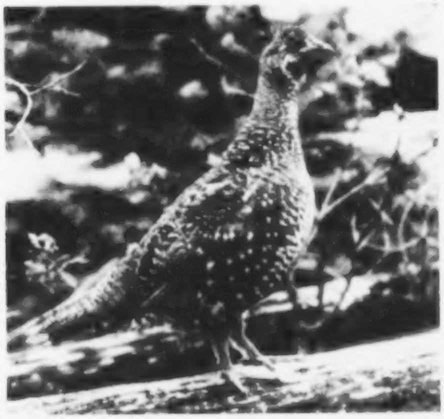
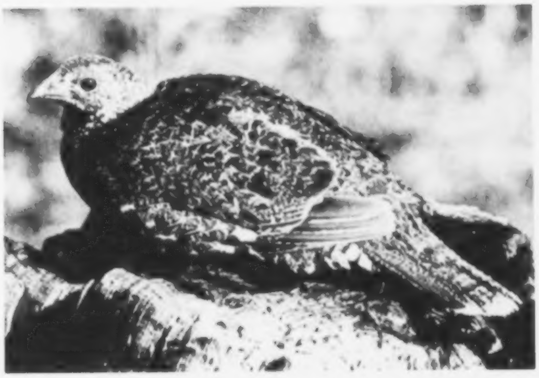


Fig. 15.4. Crouching posture.



(c) *The crouch*. If disturbed, grouse often crouch, a posture in which the bird is clearly alert and attempting to be inconspicuous. This is often the first reaction to disturbance but may be preceded by the alert posture. Feathers are smooth against the body, and the breast and belly rest on the ground or perch (Fig. 15.4). The head is drawn in upon the shoulders, crest and combs are down, wingtips project over the rump, the tail is depressed, and the overall position is horizontal. The bird usually remains motionless but may occasionally turn its head or blink its eyes (McNicholl 1978). Vocalizations are rare, but McNicholl (1978) heard a male growl from this position on two occasions, among 153 contacts with crouched males. He also noted 13 instances in which such males were as described except that heads, and in one case the crest, were raised. If pressed too closely, birds may take flight from the crouched position.

Birds also may "semi-crouch" by assuming a horizontal position with only partially bent legs and not settling clear to the substrate. This may develop into a very slow, or more rapid walk or run, away from an intruder (Mossop's (1971) Crouch and Run; McNicholl's (1978) Mobile Crouch). Very slow walking suggests the bird is attempting to flee unseen. Mossop considered crouch and run behaviour to be submissive and non-aggressive. His Fig. 7 indicates it is common among males and lone females but less common among brood hens, in which it may be overridden by distraction behaviour (15.3.3(f)).

(d) *Moribund posture*. Very sick birds often assume a moribund posture. This is a hunched stance, with the head pulled down upon the shoulders, tail down, and contour feathers ruffled. The eyes may be partially or completely closed and the wings drooped. This posture is that of a hunched resting bird except for droopy or closed eyes, ruffled feathers, and no response to an intruder. The head may droop to the front or side, and if the bird moves, it may stagger and lose balance.

15.1.2 Mobility

Mobility includes walking, running, hopping, swimming (very rare), flying, and variations of the above.

(a) *Walking*. These grouse usually walk upright in a neutral stance, placing one foot in front of the other and with the long axis of the middle toes pointed slightly inward, a slightly "pigeon-toed" gait. Speed may vary with type of activity, e.g., walking usually appears rather leisurely, but if feeding, the pace may be slower. In a slow walk, the head may move back and forth with each step. If disturbed, birds often walk in an alert posture. Speed may vary with nature of the individual (wild or tame), type of disturbance (threat or attractant), distance from disturbance, and amount of cover.

(b) *Running*. Blue grouse run well, usually in alert or crouching postures. They may run away from a disturbance or toward an attractant, e.g., a male approaching a female or a chick chasing an insect. Running appears to be accomplished more by increasing frequency of steps than length of stride. The head and neck are stretched forward more than in a walking bird.

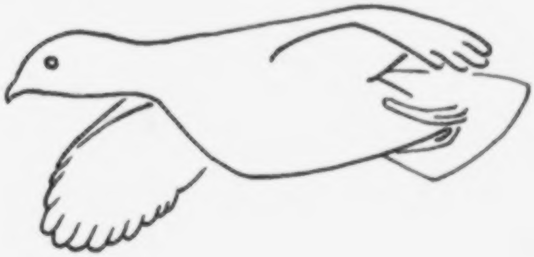
(c) *Climbing, jumping*. Grouse may step, or jump, up or down, onto or off of items such as logs or rocks, or from branch to branch in a tree. They may jump up to obtain morsels of food such as berries or leaves. Depending on distance and (or) height, it may be aided by a slight flapping of wings.

(d) *Swimming*. We know of only one instance of swimming in this bird. A hen, flushed by an observer, landed in a lake and used her wings to swim, as in a breast stroke, ~150 m to shore. Another observation involved near-swimming. A hen led her 2-day-old chicks across a small creek (Zwickel 1967*a*). Two waded across in water up to their bellies and wings. Had the water been 2 cm deeper, they likely would have had to swim, or been washed downstream.

(e) *Flying*. On breeding range blue grouse are mostly on the ground, except coastal males that sing mainly from trees. Flying is relatively uncommon and in undisturbed birds usually involves short flights into or out of trees or bushes for feeding or roosting, short flights in response to a nearby female or intruding male, or longer flights for escape. Most flights of undisturbed birds are likely short, but this is poorly documented. On winter range they are strongly arboreal and fly from tree to tree for feeding or roosting. Only rarely are birds, or their tracks or other sign (except droppings under trees) found on the ground in winter (see also 15.4.2). Flight may begin from standing, walking, or running starts, or a variety of other postures, e.g., a crouch. These grouse are strong flyers over short distances, skillfully maneuvering among trees in forested areas. Few islands more than ~2 km from a source population are inhabited, however, suggesting this is beyond the limit of sustained level flight (see also 4.2.6). This is supported by the observation above (15.1.2(d)) in which a hen that flew out over a lake came down in the water after ~150 m.

Flying usually involves steady and rapid wingbeats. Upslope flights tend to be short, perhaps best measured in tens of metres. Short ascents from the ground into a tall tree likely exceed 45° angles in some cases. Downhill flight over long distances commonly involves alternate flapping and gliding (Fig. 15.5). We watched two birds flap and glide down a gentle slope for ~2 km before dropping toward the ground and disappearing from view. A male found on Helmcken Island, BC,[4] would have had to cross at least 1250 m of Johnstone Strait from Vancouver Island (the nearest source population). This likely involved flapping/gliding downhill flight. Birds equipped with radios at Hardwicke Island have crossed saltwater channels of at least 300 m to reach mainland BC, perhaps in such flight.

Fig. 15.5. Gliding posture. Drawing by ChW Gronau.



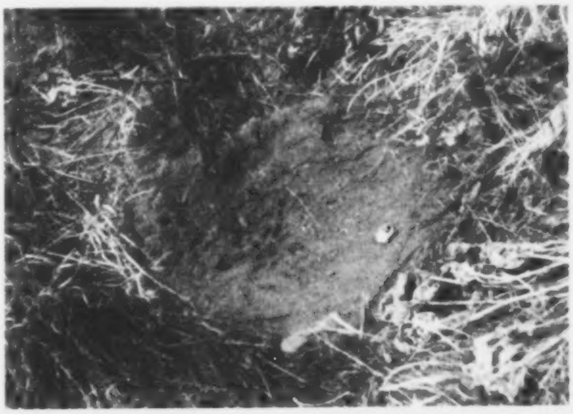
15.1.3 General maintenance

A number of what appear to be comfort and (or) maintenance behaviours have been observed. Some are rather simple and likely common in many birds, e.g., scratching and stretching, others more elaborate, e.g., dusting.

(a) *Preening*. Feathers are preened by nibbling at the feathers with the beak. Birds run their beaks around the upper surface of the tail, presumably to the preen gland, then into feathers of the breast, legs, wings, and other accessible plumage. Out-of-place feathers may be reordered without access to the preen gland. Plumage is sometimes rearranged by simply fluffing and vigorously shaking the feathers. In chicks, preening seems to begin with the loss of natal down and development of juvenal plumage.

(b) *Dust-bathing*. Evidence of dusting is common on breeding range. Dust baths (bowls) are usually in fine or sandy dry soils but occasionally in finely rotted wood of degrading logs and, especially in interior populations, in anthills (active and inactive). They are near-circular depressions up to ~25 cm in diameter (Fig. 15.6), ~2.5–10 cm in depth.[3] They sometimes contain one or two moulted feathers or one or two rectal droppings, presumably left at the end of dusting. Dust bowls are most common in summer when soils are dry, less common in spring when soils are damp; e.g., 235 were found in 1000 h of search at Middle Quinsam, May through August; only 2 in April, in 100 h of search.

Fig. 15.6. Dust bowl on shrub-steppe summer range, Frazer Creek, 26 April 1957.



In dust-bathing, the bird may scratch at the soil, then crouch, fluff its feathers, and use its legs and wings to rock itself into the substrate. It rolls onto one side, and the uppermost leg and wing throw dust over the back and tail. It then rolls to the other side and repeats the performance. The head and neck may be rubbed into the substrate, and the feet push dust under the wings. At times, the wings are flapped rapidly and billow dust into the feathers. At end, the bird stands, fluffs its feathers, and shakes vigorously. This is usually followed by preening. A hen and her entire brood of small chicks may dust-bathe, as evidenced by adult-sized bowls surrounded by several smaller versions.[5,6]

Dusting likely contributes to one or all of (1) a reordering and cleansing of the plumage, (2) a reduction in numbers of external parasites, and (3) comfort. This is a common activity in aviary birds. Birds in the aviary sometimes attempt to bathe in their water dishes (Cooper 1977), but water-bathing has not been seen in the wild.

(c) *Other maintenance behaviours*. Grouse may scratch their heads by stretching one foot forward under a partly opened wing, and bending back their head and neck. They sometimes clear materials from the side of the head by rubbing it on their back and fluffing and shaking their feathers, presumably an attempt to rearrange them. Scratching often accompanies preening.

To stretch, birds stand on one foot and extend the neck and head upwards or forward. They extend the opposite wing backwards, and the spread outer primaries may touch the ground. That foot and its toes are straightened and stretched backwards under the wing. Yawning sometimes accompanies stretching. Drinking is similar to that of other birds. To swallow, the head is tilted back and the tongue moved up and down in the mouth cavity (Cooper 1977).

Some activities are clearly related to weather. At times grouse appear to sunbathe (Caswell 1954*b*; pers. observ.), resting in open sun. On very warm days, they may seek shade, and if in the sun, they may pant, clearly hyperventilating. They are relatively immune to light rain, continuing to sing (males), feed, and perform other activities until very wet. If very wet, they may fluff and shake their feathers, presumably to shed water. In heavy rain they often seek shelter under trees, shrubs, logs, or other cover.

15.1.4 Alarm and escape behaviour

The initial reaction of many grouse to a mild disturbance is to "freeze", to become motionless and silent in the posture in which found. This is a form of escape behaviour in that many such birds are almost certainly undetected by observers or potential predators. It is often followed by an alert posture. In areas with little ground cover they often crouch until approached too closely, then flush. With more ground cover, they may walk away slowly, or run. Some individuals in some populations may pay only scant attention to an intruder and carry on with whatever activity they are engaged.

The distance at which a bird flushes, the flushing distance, and distance flown vary among individuals, populations, and habitat. A range in mean flushing distances of ~11–13 m at Copper Canyon differed from those of ~6–8 m at Comox Burn and Middle Quinsam (data extrapolated by us from Mossop's (1988) Fig. 1.9). Hens with broods had the shortest flushing distances at all areas. They were least likely to fly out of sight (Table 15.1) [1], then males found hooting [2], with no difference between lone females and silent males [3]. We also have worked with other populations and in which birds varied from relatively tame, at Skalkaho and Frazer Creek, to very wild, at Duck Creek. See 15.3.3(e) and (f) for more specialized alarm and escape behaviours of hens and young chicks.

Table 15.1. Grouse that flew out of sight on first flush (%), Comox Burn and Tsolum Main, 1971 and 1972.

	n	Out of sight
Lone females	22	75
Silent males	383	73
Singing males	231	55
Brood females	196	18

Birds that flush often take refuge in nearby trees, but this depends on the direction from which an intruder approaches relative to location of a tree, or trees. Distances flown are determined in part by distance to a tree(s). In the absence of nearby trees, birds may fly until they find other cover in which to take refuge, e.g., thickets or dense ground cover. They may disappear behind low hills or settle into riparian shrubs in valley bottoms. In open landscapes, such as shrub-steppe, large clear-cuts, and subalpine areas, flights tend to be longer than in forested habitats. Except when flying into nearby trees, flights tend to be downhill or along contours.

We have a few observations on reactions of grouse in flight to aerial predators. For example,

> Grouse may outfly raptors. A half-grown juvenile outflew a bald eagle (*Haliaeetus leucocephalus*), and a hen outflew a Cooper's hawk (*Accipiter cooperi*), both in level flight. A bald eagle stooped on a hen in flight, but she veered sharply and escaped. A red-tailed hawk (*Buteo jamaicensis*) stooped on a male on the ground in open shrub-steppe habitat, but the grouse flushed just before its arrival and flew off. The hawk returned to soaring.
>
> Grouse may drop to the ground when pursued by raptors. Two males, one flushed under a golden eagle (*Aquila chrysaetos*) and another under a goshawk (*Accipiter gentilis*), made short rapid flights, landed quickly, and disappeared into cover (DH Mossop, pers. comm.; pers. observ.). Another goshawk pursued a flushed male, the grouse accelerated its flight for about ~100 m, dropped into a willow thicket, and the hawk flew on. In a similar incident, a yearling male pursued down a gentle slope by a northern harrier (*Circus cyaneus*) suddenly altered its flight by dropping almost vertically, ~5–6 m into a serviceberry thicket; perhaps because the harrier was gaining. The harrier overshot the thicket and flew on. When approached, this grouse was flattened to the ground and so traumatized we picked it up.

Raptors, or other potential predators, may elicit "hiding" behaviour. For example,

> A brood hen crouched on a log when a northern harrier flew over quickly dropped to the ground beside the log and resumed her crouch there, presumably an attempt to reduce

conspicuousness. An adult male crouched on a log and that was under observation to read his bands suddenly tilted his head as if to examine the sky. A bald eagle was soaring high overhead some 200–300 m away. The grouse clearly had his eye on this bird, dropped to the ground, and resumed his crouch there. DH Mossop (pers. comm.) observed an adult male, chased by a goshawk, land and crouch under a log. He approached and picked it up.

Clearly, some raptors elicit extreme alarm behaviour in blue grouse.

Grouse that run from an observer usually flush when pressed too closely, but if they cannot fly because of injury, they may hide under a log or other cover. In one incident a goshawk struck a hen on the ground and flew off when we appeared. This hen, with a few slight lacerations and apparently in shock, crouched and allowed us to pick her up. On release she ran under the nearest log and crouched there.

Grouse often must make choices when confronted by predators, often split-second decisions. In the longer view, they also must choose habitats in which to live that provides security commensurate with other requirements. This is undoubtedly an important component of the "settling response" (Hilden 1965), a behaviour most often of young birds at termination of natal dispersal.

15.2 Males

There are two classes of males on breeding range, those with territories, mainly adults, and those without, mainly yearlings. Behaviours and home ranges of these groups differ markedly, with differences principally related to territorial status. Since most yearlings do not have territories and most adults do (Bendell and Elliott 1967), we consider males by age class in most instances.

Male blue grouse are generally classified as promiscuous, with territories widely dispersed (Bendell and Elliott 1967; Hjorth 1970; Wiley 1974; de Vos 1979). A few authors have reported communal, lek-like, display (Schottelius 1951*a*; Caswell 1954*b*; Blackford 1958, 1963; McNicholl 1978), but Lewis (1985*a*) argued that all instances described as lek-like can be explained alternatively. Bendell and Elliott concluded that males have dispersed territories, principally because they remain on them throughout the breeding season. We agree with this interpretation, and with Lewis, that evidence is insufficient to suggest this species forms leks.

15.2.1 Vocalizations

Adult and yearling males have three (Stirling and Bendell 1970), perhaps four, distinctive calls, one of which, the "hoot", is true song (McNicholl 1978). The hoot and "whoot" are clearly reproductive in nature, while the "growl" has been described from aggressive encounters between males (two variants may represent different calls). Since all are used by both yearlings and adults, we describe them here but consider their uses within sections on behaviour of the age classes. Other sounds reported only from aviary males include a "ko-ko-ko" (the "cough" of Stirling 1965; perhaps the softer variant of the growl reported in the field (15.2.1(c)), a "grunt", "hiss", "purr", "sneeze note", "rattle" (or rutututut, perhaps a modified growl), and "gluck" (Cooper 1977). Since these have not been reported from the field, their meaning is difficult to discern, and we leave their analysis to a future, more comprehensive consideration of all aviary behaviour.

(a) *Song*. Hooting is a multiple-syllable low-frequency song, the Multiple Hoot Canto of Hjorth (1970). It is perhaps as low in frequency as that of any grouse and clearly differs between interior and coastal subspecies of blue grouse. Expressed as words, that of a coastal male closely approximates "*a humph humph humph, humph, a humph humph*". Hjorth (1970) found fundamental frequencies of songs of interior males to range between 50 and 100 Hz, those of coastal males between 110 and 150 Hz. Degner (1988) found hooting in a population of *D.o. pallidus* to range between 100 and 110 Hz and that in three populations of *D.o. fuliginosus* and one of *D.o. sitkensis* to range between 110 and 175 Hz, tending to increase from south to north. Owing to low frequency and volume, songs of interior birds are reported to be audible to humans only up to 30 m (Rogers 1968), 40 m (Hjorth 1970), or 75–100 m (Musschl 1963*d*). We think Musschl's estimate is most accurate, but only under ideal listening conditions. Songs of coastal males are much louder, often audible beyond 300 m (Stirling and Bendell 1970), up to 500 m (Hjorth 1970). Differences in amplitude may be an adaptation to open (interior birds) versus more heavily forested habitats. In general, however, low frequencies (interior birds) attenuate less than high frequencies (Wiley and Richards 1982) and should be preferred in forested environments, which runs counter to the more open versus more forested habitats of interior and coastal grouse. Wiley and Richards note that our understanding of sound attenuation in nature is a complicated and as yet an unresolved problem that is affected by atmospheric turbulence and scattering by vegetation. Whether differences in amplitudes and frequencies of songs of interior and coastal birds are habitat-related adaptations is not clear but deserves study.

Number of syllables per song also differs between interior and coastal males. Those of interior birds most often have five syllables, coastal birds, six (Hjorth 1970; Johnsgard 1983; Fig. 15.7) [4]. Interior birds deviate little from five syllables, coastal birds more so from their dominant six-syllable songs. From this, Degner (1988) suggested interior birds tend to have only one song type, coastal birds more than one. Where coastal and interior races merge there is more variation (Table 15.2[7]), but most songs are of five syllables, suggesting this is the dominant type. In all groups, those with <5, 1–4 (Table 1, paper 3, in McNicholl 1978), tend to be initial songs, with most individuals soon changing to five or six syllables.

The first syllable of each song is of lower frequency than the second, with a gradual decline in those that follow (Fig. 15.8). The last is about the same as the first (Degner 1988). In interior males, the last two are "double" according to Degner and sonograms in Hjorth (1970). In six- and seven-syllable songs of coastal males only the fifth is double (McNicholl 1978). Intersyllable lengths tend to decrease from the first to last. Songs of interior males are ~2.5 s in length, those of coastal males, ~3 s.

On Vancouver Island, songs per minute range from 1 to 10 ($n = 89$ males; Stirling and Bendell (1970)) and vary with excitement of the male (Bendell and Elliott 1967). Songs of three *D.o. pallidus* in northcentral Washington ranged from

Fig. 15.7. Frequency (%) of song types (number of syllables) of *D.o. pallidus* (samples from northcentral Washington and Montana combined) and of coastal (*D.o. sierrae*, *fuliginosus*, and *sitkensis* combined) males. Sample sizes are number of songs, with number of birds in parentheses.

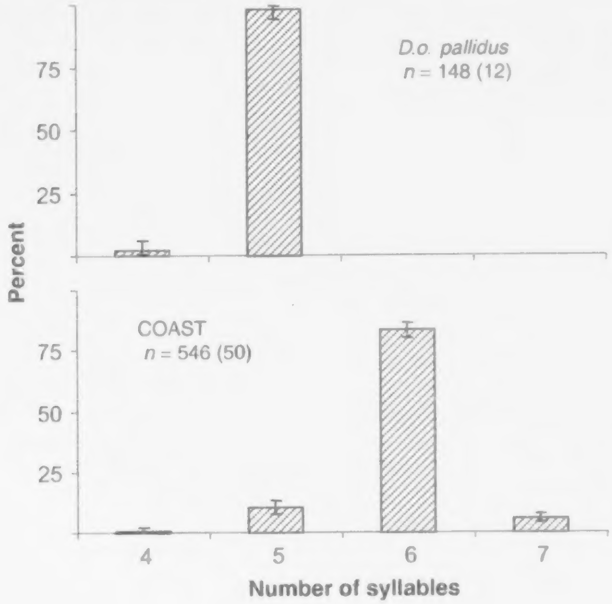


Table 15.2. Number of syllables per song (by %) in two apparent coast–interior "hybrid" populations.

			Percent of songs		
			No. of syllables		
Hybrid type	n_{bird}	n_{songs}	4	5	6
D.o. sierrae × *D.o. pallidus*[a]	11	110	10	81	9
D.o pallidus × *D.o. fuliginosus*[b]	9	90	0	76	24

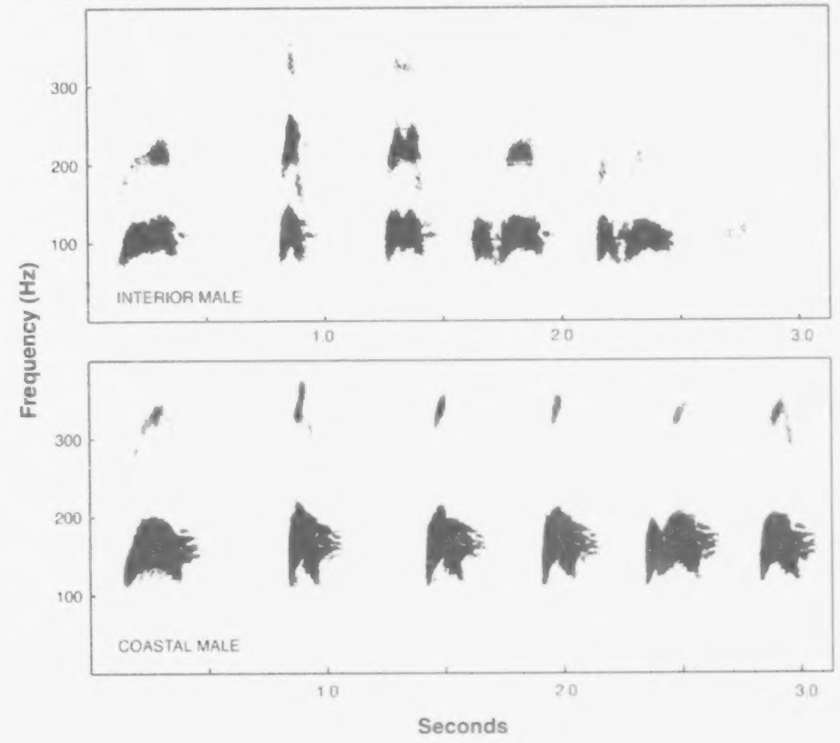
[a] Yakima and Kittitas counties, Washington.

[b] Hart's Pass area, near crest of the Cascade Mts., northcentral Washington.

2 to 6 per minute. Those of six *D.o. sierrae* in westcentral Oregon ranged from 1 to 8 per minute. Individuals also may vary the volume of their songs (Bendell and Elliott 1967; McNicholl 1978; pers. observ.). Variations in songs per minute and volume may relate to differences among males, time of day, season, level of excitement, or disturbance.

(b) *The whoot.* This is a courtship call (the "oop", or "love-note", of Brooks (1926, p. 281), the "precopulatory hoot" of Hjorth (1970, p. 277)). It is given at the end of a rush toward a hen—a display referred to as the "rush cum single hoot" by Hjorth (p. 274) or the "rush and whoot" by Stirling and Bendell (1970, p. 164). These authors report it to be a double-note

Fig. 15.8. Five- and six-syllable song types of interior and coastal males: interior male at the Methow Game Range, WA; coastal male at Hardwicke Island, BC. Recordings and sonograms by MA Degner.



call, with a fundamental frequency of ~200 Hz, higher than that of the hoot. The second note is said to be very short and only heard if the observer is very close. Bendell and Elliott (1967, p. 17) described the second note as a "squeal" and thought it might result from a sucking in of air after expiration of the courtship note. Hjorth (1970, p. 278) described it as a "high frequency whistle note" that might reflect a sudden exhalation of air. Degner (1988) considered the whoot as a single note call and detected no second note in sonograms from coastal and interior males (Fig. 15.9).

The whoot is much louder than hooting and under appropriate conditions can likely be heard at >0.5 km in interior and coastal males. In contrast to the hoot, Degner (1988) found no clear distinction in frequency or length between whoots of interior and coastal birds [he thought those of interior males might be highest in frequency and longest, but samples were small]. Shapes of the spectrograms are certainly different, with that of interior birds having no harmonic and that of coastal males with a clear harmonic. Nevertheless, we have detected no difference by ear, and both are given in the same context, at termination of the rush and whoot display (see 15.2.3 (g)).

(c) *The Growl*. The growl was first described by Bendell (1954, p. 49), as a rapid "gugugugugug". It was thought by Bendell and Elliott (1967) to sound like the growl of a dog given in short staccato phrases—the "growl call" of Stirling and Bendell (1970, p. 168), the "harsh staccato cantus" of Hjorth (1970, p. 281).

Although not well documented, there appear to be two variants of this call, perhaps two different calls (Zwickel 1992). That depicted in Fig. 15.10 is the aggressive version, given in an encounter between two males. What appears to be a softer and slower 'gugugug' is sometimes given by males when disturbed by an observer, sometimes in response to simulated wailing of small chicks, and usually as the male walks away. It may reflect a conflict between aggression and fear, fight or flight. Because of their similarity these vocalizations have usually not been separated by observers in the field. Owing to the contexts in which they are given, we suspect they are different calls. Both occur in disturbance situations. Sometimes calls are generally similar and blend in to one another. They may vary in volume, length and intensity, making differences difficult to define.

Males may growl throughout their time on breeding range, but we have no data from winter range. They growl throughout the year in the aviary, mostly in spring (Cooper 1977).

15.2.2 Yearling males

(a) *Sociality*. We define sociality as the tendency of an individual, or individuals, to associate with conspecifics. As a measure of sociality, we examined all sightings of yearling males at Hardwicke Island from 1979 to 1984 as to whether these birds were alone (≤10 m from another bird) or with another bird. Prior to the main breeding period, on or before 22 April, 91% (41/45) were classified as alone. During the period in which virtually all breeding takes place, 23 April–1 July, 95% (94/99) were alone, not significantly different from the earlier period [5a]. After 1 July, when many yearling males are leaving summer range, 77% (34/44) were alone, significantly fewer than in the earlier samples combined [5b]. Among all contacts with yearling males throughout spring and summer (n = 188), 90% were alone.[7] Clearly, these birds tended to, at the very least, be temporally separated from other individuals while on summer

Fig. 15.9. Whoots of an interior and a coastal male: interior at the Methow Game Range, WA; coastal from Adam River, Vancouver Island. Recordings and sonograms by MA Degner.

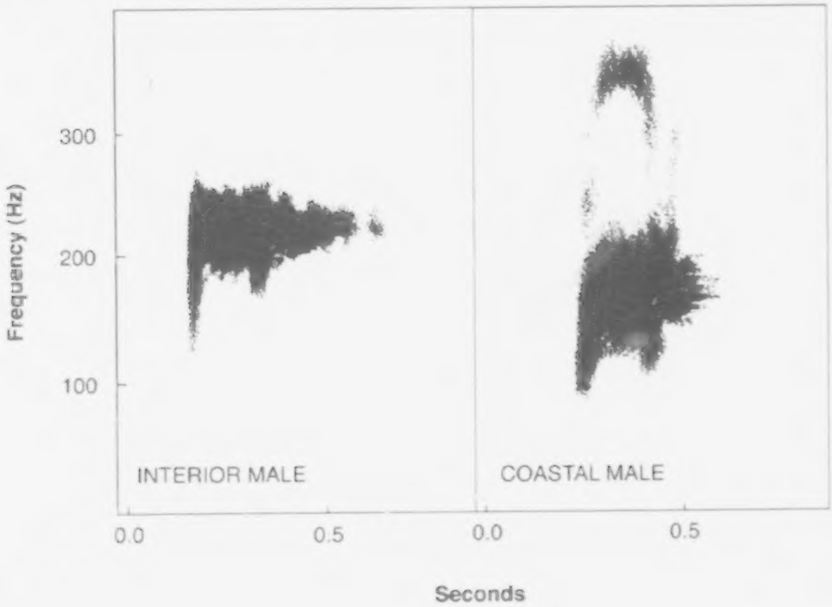
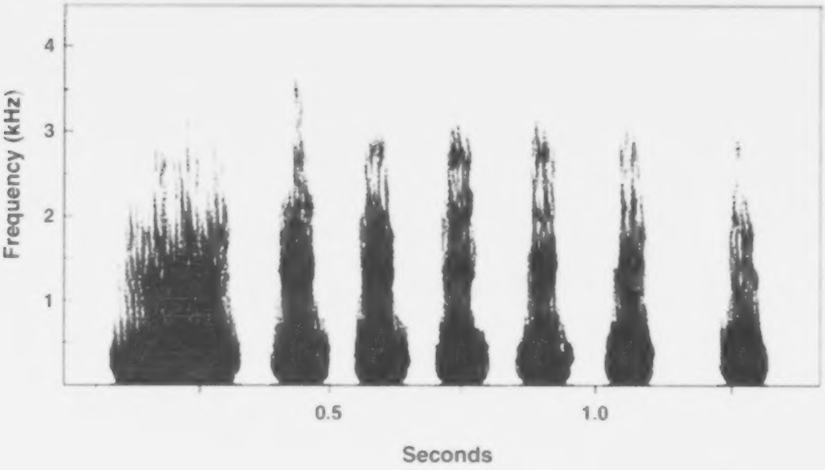


Fig. 15.10. Growl call of an aviary male, *D.o. fuliginosus*. Recording and sonogram by I Stirling.



range. Increased association with other birds in mid to late summer suggests a weakening of antagonism among individuals and may reflect a tendency to flock prior to moving toward winter range.

Among nine cases in which yearlings were classified as with other birds prior to 1 July, three were with a male, five with a female, and one with a male and female. After 1 July, individuals were classified as with a male 15 times, a female 9 times, and a male and female 5 times, not significantly different from the earlier time period. In some cases these may have been chance occupations of a common area, not real associations.

(b) *General activity patterns.* Yearling males were usually in or near thickets during the day at both Comox Burn and Hardwicke Island, tending to move very little.[8] At Hardwicke Island, radio-marked yearlings were found in the open (away from vegetative cover) only 30 (18%) of 171 times (Jamieson 1985). Fifty found twice in the same day moved a median distance of only 2 m/h, with most daytime hours spent in or near thickets (Jamieson 1982). Activity increased at dusk. Feeding and other activities occupied 50% of their time in the 2 h before sunset, only 28% around midday. At dusk, they sometimes ran in short bursts of 5–15 m or made 10–30 m flights for no apparent reason. Twenty-three of 29 interactions with conspecifics (79%) occurred within 1 h of sunset. These observations agree with reports of yearling male behaviour at Lower and Middle Quinsam (Bendell and Elliott 1967) and with observations at Comox Burn.

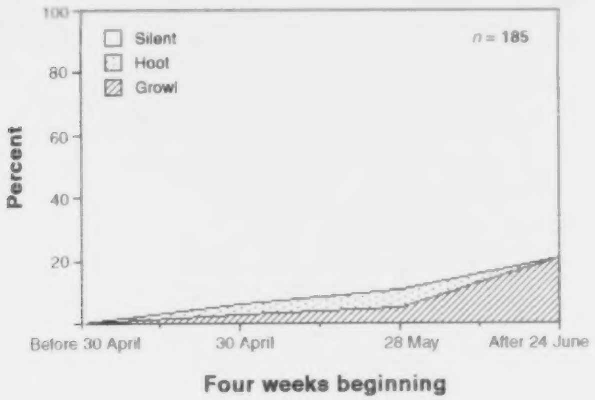
During 126 h of observation of yearling males at Hardwicke Island, 74% of their activities were classified as "stationary" (moves of <1 m/min), the remainder as "moving" (Jamieson 1985). Moving included three principal activities: feeding, interacting with conspecifics, or walking. Approximately one-third of walking time was devoted to feeding.

Yearling males rarely occupy territories (Bendell and Elliott 1967; Lewis and Zwickel 1981) or sing, and those that do, appear to sing less and abandon breeding range earlier than older males (Bendell and Elliott 1967). At Lower Quinsam, among >300 contacts with males identified as territorial, only one was a yearling (Bendell 1955*a*). At Middle Quinsam, Bendell and Elliott (1967) estimated that 11% of territorial, or hooting, males were yearlings, but all that sing are not territorial (see below). Removal experiments there at the time (Bendell and Elliott 1966) may have increased the number found hooting.[9] Among 223 contacts with adults, 77% were singing, among 56 contacts with yearlings, 30% (data extracted by us from Table 5 of Bendell and Elliott 1967), a significant difference between age classes [6].

Among 24 radio-marked yearlings at Hardwicke Island, only one behaved as if territorial (Jamieson 1985). His home range was smallest of all yearlings, 0.6 ha, and similar to that of territorial adults. He sang throughout the day for 6 consecutive days, but abandoned his territory between about 15 and 20 May (Jamieson 1982), very early for a territorial bird. Six clearly non-territorial yearlings were observed singing, one at two different times. Singing was brief, soft and sporadic at first and only at dusk, but more continuous and louder with time. Bendell and Elliott (1967) and McNicholl (1978) also noted that yearling song tends to be low in volume. We suspect singing by non-territorial yearlings is elicited by association with singing adults or encounters with females. Bendell (1955*a*) saw a yearling display and hoot when a female landed nearby, but the male soon left.

Yearling males seldom vocalize (Fig. 15.11). Among 129 banded yearlings at Comox Burn, only 6 were known to have hooted. When yearlings sing it tends to occur after the main breeding period (4/6 instances after 15 May), perhaps reflecting increasing maturity in these birds and (or) decreasing pressure from adult males. No yearling was found hooting on more than one occasion. Growling, too, was uncommon among birds in this sample and heard from only nine individuals, one of whom growled on two separate occasions. There appears to be a tendency for this call to increase in late summer, but most that were recorded were in response to our intrusions and might relate to increasing maturity and aggressiveness. In no case was an individual known to have both hooted and growled, and we know of only one instance of a yearling that whooted.[10]

Fig. 15.11. Vocalizations of yearling males (% vocalizing), by date.



(c) *Interactions with conspecifics.* We have few observations of yearling males interacting with conspecifics, partly because of their secretive behaviour. As noted in (a) and (b) above, these involve encounters with territorial adult males, other yearling males, females, and situations in which males and females were present.

Among nine radio-marked yearlings at Comox Burn whose home ranges encompassed areas where territories of adult males were well documented, each was associated with, on average, four territories of adult males (Sopuck 1979). These birds were found outside territories of adults more often than expected by chance. Sopuck suggested (p. 18–19) they ". . . may be avoiding, or are driven from, territories of adults". Those at Hardwicke Island also tended to associate with territories of adults (median no. of territories = 2, range = 0–6; Jamieson and Zwickel 1983*b*). They were closer to territories than expected by chance but not necessarily on them. Some settled near vacant territories that were occupied in previous years, indicating that resident adults may not be necessary to elicit a settling response in young males.

Hooting of territorial adults may attract non-territorial yearlings (Bendell and Elliott 1967), providing opportunities for encounters with them. Yearlings at Hardwicke Island made direct movements of up to 250 m toward territories on which resident males were singing on eight occasions (Jamieson 1985). In other cases they were feeding or moving through an area when confronted by a resident adult. In 25 encounters between yearling and adult males observed by Jamieson, all resulted in agonistic interactions. Adults ran or flew toward the younger birds and assumed threat postures. The younger birds almost always assumed neutral or submissive postures. In 10 cases yearlings almost immediately flew off, in 14 they were displaced by rushes from adults, and in another, an adult physically attacked a more persistent intruder, removing several feathers.

Yearling males were seen to interact with both females and territorial males in five cases at Hardwicke Island (Jamieson 1985). Here, yearlings flew up to 100 m toward females that were calling on or near territories of resident adults. Residents courted the females only after chasing off the intruders.

Bendell and Elliott (1967) found yearling males at Middle and Lower Quinsam to both court and show no interest in females in spring, but provided little information on their courting behaviour. At Hardwicke Island yearlings were seen to interact with lone females on 11 occasions (Jamieson 1985). In five cases, they flew or walked toward hens that had been calling, in five others they encountered them while moving about, and in one, a male flew to a hen that had landed nearby. On approaching females, yearlings sometimes assumed full or partial display and bobbed their heads, but did not drag their wings or whoot as adults usually do. On three occasions they suddenly moved away from the hen and pecked at bushes. None attempted to mount, for even after up to 5 min of courtship, they ceased to display and began to feed. Late in the breeding season, two yearlings showed no interest in nearby females. In seven instances in which the hen's behaviour was monitored, none seemed to show an interest in the male. From these observations, Jamieson (1985, p. 75) concluded that non-territorial yearlings ". . . did not express the full range of courtship responses shown by territorial males." He suggested failure to show a full range of mating behaviours may reflect (1) immaturity, (2) unreceptive responses by the female, or (3) lack of possession of a territory. Most interactions with adult males and females occurred at dawn or dusk and declined as the spring–summer season advanced (Jamieson 1983*a*).

Interactions between yearling males appear to be rare. In 126 h at Hardwicke Island in spring, Jamieson (1982) observed such interactions only four times, all of which were agonistic. One involved a physical fight that included growling, wing buffeting, and jumping at each other with their feet. In all cases, one was driven off by the other. Two were found together six times in summer with no antagonism observed, suggesting agonistic tendencies had waned as the season progressed.

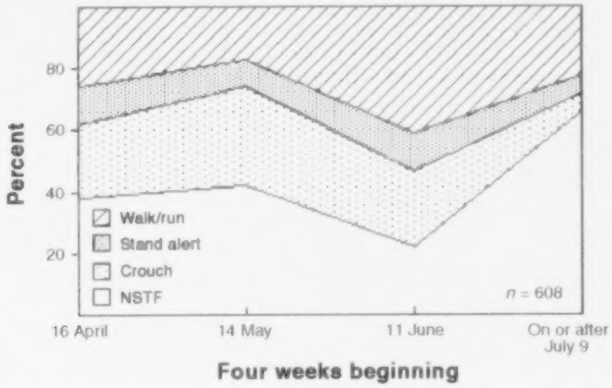
15.2.3 Adult males

(a) *Sociality.* Adult males on breeding range are spatially antisocial among themselves, as indicated by near-exclusive use of space at this season. Males that intrude into territories of others are driven off if detected by the resident (Bendell and Elliott 1967). In an April to August sample at Comox Burn and vicinity, 97% of 715 observations of males were of single birds (>10 m from another grouse), only 10 were with another male (Zwickel 1992). This sample included yearling and adult males, with sightings biased toward daylight hours. With more dawn and dusk sightings it would almost certainly change some, but likely not to a great degree.

Although usually alone, territorial males have strong auditory associations with neighbors (Bendell and Elliott 1967; McNicholl 1978; Falls and McNicholl 1979). Hooting by one often elicits singing by neighbors (see (d), below) and ". . . likely informs males of the proximity of their neighbors . . ." (Stirling and Bendell 1970, p. 163). This seems to contribute to the formation of singing groups and to keeping individuals apart, thus containing elements of both social and antisocial behaviour.

(b) *Response to human intrusions.* When first alerted to our presence, many males either flush before we see them (escape) or crouch (hide, Fig. 15.12[11]). Initial behaviour changes as the season progresses. Males are most likely to flush or crouch up to ~11 June and to flush, walk, or run up to 9 July. Compared to lone females (see Fig. 15.18), males are less likely to flush

Fig. 15.12. Behaviours of males (yearlings and adults combined) when first seen, by 4-week periods, Comox Burn, 1971 and 1972. NSTF, not seen till flushed.



before being seen prior to 9 July [7a–d]. Clearly, territorial males hold their ground more strongly than lone females.

(c) *Singing*. One of the most conspicuous behaviours of males on breeding range is hooting and, along with courtship display, has been described in detail by Hjorth (1970), Stirling and Bendell (1970), and McNicholl (1978). We base our descriptions of these behaviours principally on observations of these authors. For use of songposts see 16.3.2.

"Routine hooting" (Fig. 15.13) involves little display. The body is held at an angle of about 45°, with the head extended forward and slightly downward. The crest is down and the combs neutral, showing a trace of yellow. The neck region is expanded by partly raised neck feathers and inflation of the esophagus. Lateral cervical apteria are not visible, and white-based feathers surrounding the apteria may, or may not, show as thin white lines on each side of the inflated neck region. Wings are held closely to the sides, the tail is not fanned,[12] and is usually held down or approaches the horizontal. Each song is initiated with the bird opening, then closing its beak, presumably taking in air to inflate the esophagus, air sacs, and lungs. The first note immediately follows closing of the bill, the head nods up and down, the expanded neck region pulsates, the tail moves up and down slightly, and if exposed, the white feathers on the neck may flash briefly with each syllable. If cervical apteria are exposed the surrounding white feathers pulsate with each syllable. Males also may hoot in most phases of courtship display (Stirling and Bendell 1970).

Fig. 15.13. Posture during routine hooting. Photo by Reto Zach.

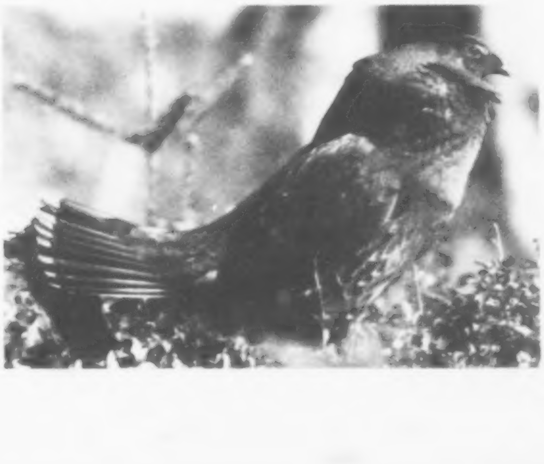
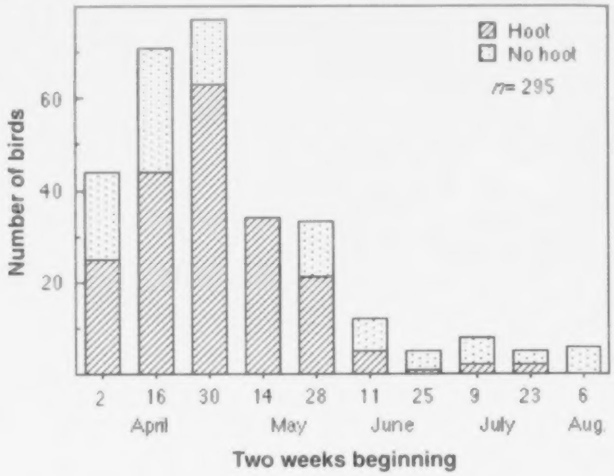


Fig. 15.14. Numbers of males found hooting or not hooting, by 2-week periods, Hardwicke Island, 1981–1983.



Singing varies seasonally, beginning in lowland coastal regions in late March and early April, increasing through April and to mid May, declining steadily to mid June, and is virtually over by early August (Fig. 15.14). Between late April and early July, this pattern of singing generally follows that for copulation (Fig. 10.1) but begins earlier and persists in a few males that remain on territory into early August, rarely early September. Most adult males found up to early June on lowland Vancouver Island are singing; most after that are not, but specific dates will vary among local populations.

Hooting also changes with time of day. At Lower Quinsam, morning hooting began well before sunrise, at a time when light could not be measured on an exposure meter. Intense activity continued until a light level of 2–4-foot candles (Bendell 1955*a*). Intense evening singing began between 2- and 4-foot candles and continued beyond a zero reading on a light meter. Morning and evening activity tended to become progressively earlier and later as the season progressed, likely in relation to light levels.

Beginning in late April and to about the end of May, many males sing throughout the day on Vancouver Island (Bendell 1954; McNicholl 1978), with most frequent and continuous singing in morning and evening. By June, daytime singing is sporadic, with most intense hooting in the morning and evening on most days. Occasionally birds sing throughout the day at this time, but what triggers this change has not been studied; McNicholl (1978) suggested birds may sing more frequently on cloudy than sunny days. General observations indicate seasonal singing drops off more rapidly on interior shrub-steppe ranges, where summer temperatures are greater than in coastal areas. We suspect that a seasonal decline in libido, coupled with warm weather, contributes to a depression in singing.

Rarely, males may sing in full darkness, even with complete cloud cover. We have at least 13 records of hooting between 0315 and 0435 h, 1 at 2030 h, 1 at 2320 h, and 1 at 0130 h, with our notes indicating complete darkness in all cases. All were between 13 April and 4 June, the principal breeding period.

There is considerable variation among individuals in singing tendency (McNicholl 1978). At Comox Burn, among 34 banded individuals, 1 male was hooting in only 16% of McNicholl's 16 encounters with him, another in 72% of 60 encounters. Others ranged between these extremes; most (79%) between 40% and 72%.

(d) *Group song.* Males often sing in groups, usually involving 2–3 birds, but up to 7 (McNicholl 1978) or 8 (Bendell and Elliott 1967). Among 123 birds found hooting on Comox Burn in 1 year, in only five cases could no others be heard (McNicholl 1978). McNicholl reported (p. 86), ". . . initiation of hooting by one bird was rapidly followed by the commencement of another from the same direction, and . . . the cessation of singing by one was followed rapidly by . . . [that] of another". If one of a pair of hooting males altered its rate of singing, the other always altered its rate ($n = 131$). Within singing groups, one individual was consistently dominant, as indicated by his early morning initiation of song, a tendency to sing more persistently within that group, and, if in a trio, at a faster rate than the others. On given mornings ". . . different groups often began singing at different times, emphasizing this intragroup association" (McNicholl, p. 88). Observations and experimental playbacks demonstrated that singing of one bird is influenced by that of its neighbors. Group song may represent counter-singing.

(e) *Functions of song.* Hooting appears to function as an advertisement that attracts hens and informs other males of the proximity of their neighbors (Bendell and Elliott 1967; Stirling and Bendell 1970; McNicholl 1978). If, during routine hooting, a female appears within or near a male's territory, he usually stops singing and goes into "feather spread", a part of courtship display (see (g), below). If spurned by the hen, he may hoot briefly while in feather spread, but soon returns to routine singing. Hooting seems more of a preliminary to courtship than a direct part of it. Males also discriminate between songs of strangers and neighbors in the correct direction (Falls and McNicholl 1979), likely contributing to the maintenance of territorial space. Although non-territorial yearlings may be attracted by the song of males (Stirling and Bendell 1970), this is likely not a specific function of it.

(f) *Non-vocal displays and sounds.* Males produce two distinctive mechanical flight sounds, "landing on loud wing" and "flutter flights". Judging from contexts, both appear to have advertising functions.

Except initial bursts into the air, flying and landing are usually relatively quiet. However, territorial males often land with exaggerated wingbeats ('landing on loud wing'), producing a distinct ripping sound (Bendell and Elliott 1967) that carries much farther than normal landings, likely ≥100 m.[13] Such landings are common and appear to be produced principally by territorial males [8],[14] but have occasionally been reported in females. In males, this appears to be associated with short flights, usually within a bird's territory. It may be produced by a bird flushed by an observer or one that flies toward an attraction such as a female or her cackle (see 15.3.1(b)). At Mt. Lassen, CA (*D.o. sierrae*), and the May Ranch (*D.o. fuliginosus*), where males sing mainly from trees, they often fly to a nearby tree and land on loud wing in reaction to playbacks of the female cackle call. We think this is mainly an advertisement, "I am here" or "this is my territory". It may have both advertising (to females) and defensive or warning connotations (toward males and other intruders).

Flutter flights were first described by Green (1928) and elaborated on by Wing (1946) and Blackford (1958, 1963), all working with *D.o. richardsoni* or *D.o. pallidus*. Wing (p. 154) described this display:

> "There seem to be no preliminaries to the flight; the bird springs into the air, the wings beat rapidly and loudly as he rises, there is a pause as the bird coasts on set wings and starts to descend, then a last burst of the wings occurs as he approaches the ground . . . In all cases . . ., the hooter reached a height of about a yard and alighted within a couple of yards or so of the starting point. Some flights rotate to the right, but most . . . rotate to the left in an arc of about 180°."

The sound from this display certainly announces the position of a territorial male, for under appropriate conditions we estimate it can be heard for ≥400 m. Wing (1946) reported that drumming flights (our flutter flights) began before dawn, ceased about daylight, resumed late in the day [evening], and ended between about 1900 h and 2000 h in the Grand Ronde River area, OR. Although males may hoot throughout the day, he observed no flutter flights except in the morning or evening. This is in general agreement with our observations in a number of different interior populations. We have, however, occasionally heard flutter flights in midday, presumably in response to encounters of males with females or their calls, and we have elicited them in midday with playbacks of female cackle calls.

Flutter flights may be elicited by wingbeats of nearby grouse (males or females), especially by other males performing such flights; female cackles or playbacks of same; or perhaps, detection of approaching females. They are usually associated with hooting. A burst of flutter flights as the day begins is similar to the dawn chorus of passerines, for it terminates soon after daybreak. Field notes from 10 April 1994 in the Methow Valley (about the beginning of peak breeding in this area) provide an example of this phenomenon:

> "We go to Lester Spring to try and record FFs [flutter flights]. Arrive about 0445 h; dark on arrival. Hear 1st hooting ~0500 h. Start hearing FFs. Male worked yesterday seems to be hooting; gives FF. Hear cackle near spring. Work toward hooting male. See him give FF on ridge above us against brightening sky. He hoots and displays; FF. Now hearing FFs, cackles, and whoots from all around us—likely at least 10 different males—out to ~1/2 km."

We left the area at 0610 h, by which time there was full daylight, and most flutter flight activity had ended.

The female cackle functions as a powerful stimulus for inducing flutter flights in interior males for among 32 flutter flights immediately following a natural or recorded sound,[15] 3 were induced by flights of nearby females, 1 by clucking of a brood hen, 3 by cackles of wild females, 1 by playback of a female whinny (Stirling and Bendell 1966), and 24 by playbacks of female cackles. Eighty-four percent followed cackles of wild females or playbacks (75%) of this call. Many flutter flights appear to be induced by those of nearby males, for if one male does so, a series often can be heard moving across the landscape, one immediately after, sometimes overlapping, another.

Coastal males also produce flutter flights, but they are less complex and softer than those of interior birds. Here, where males in natural forest usually sing from trees, the display consists of a short flight from one tree or branch to another. It differs from landing on loud wing in that exaggerated wingbeats are given throughout the flight. In situations where coastal males sing from the ground, e.g., on clear-cuts, flights are short (perhaps 2–3 m long, 1–2 m high) and straight, lacking the curve of interior birds; although Bendell saw one that resembled that of an interior male. Straight flights may be an adaptation to the usual arboreal songposts of coastal males for a curving flight might make landing on a limb difficult.

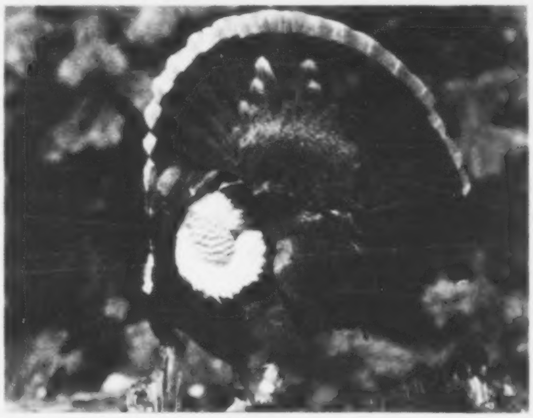
These flights appear to be less frequent in coastal than interior subspecies. During a series of eight evening hooting counts at Comox Burn (four stations per evening and at peak breeding) we recorded means of 112 hooting cantos, 12.8 whoots, and 0.4 flutter flights per 10 minutes of listening.[16] A mean of five males per station was reported each evening, but this was based only on birds that could be individually isolated.[17] Although we have no comparable counts from interior ranges, we think numbers of evening flutter flights per unit of time would greatly exceed those of coastal males in areas of comparable population density. Perhaps the loud, frequent, and more complex flutter flight of interior males functions as a supplemental advertisement to the soft hooting of these birds.

This display appears to function as an advertisement to females at a distance, not as part of courtship. For example, in 22 instances in which we saw interior males perform flutter flights, no female was found in the near vicinity in 13 cases, even though we were working with pointing dogs. In the other cases, nearest females were ≥10 m from the male, too far, in our view, to be considered as being courted. Lumsden (1965), working with sharp-tailed grouse, suggested that flutter jumping in lek grouse is used to advertise the location of strutting grounds, for he never saw a male perform this display when a hen was in his territory, and seldom when in nearby territories. We think this display is principally a locational advertisement, not a direct part of courtship.

(g) *Courtship*. The courtship display of males is striking, leading JS Newberry to exclaim "The cock is decidedly the handsomest of all American Grouse, . . ." (Coues 1874, p. 398). Depending on the situation, courtship display " . . . consists of 3 phases: the *feather spread*, the *rush and whoot*, and the *head bob*" (Stirling and Bendell 1970; p. 164).

A territorial male may erupt into feather spread (Fig. 15.15) on seeing a female, or dummy female nearby; hearing a female land, whinny (15.3.1(b)), cackle (15.3.1(b)), or cluck nearby, including playbacks of the calls; seeing another male nearby; hearing a male hoot or whoot nearby, including playbacks of the calls; or on being approached by an observer. A bird in full feather spread initially stands upright, has fully erect, yellow combs, bulging neck region with fully exposed lateral cervical apteria surrounded by rosettes of white feathers, slightly drooped wings, extended alulae, fully fanned and vertically erect tail, with feathers of the crissum erect. The tail may be cocked toward the head, beyond the vertical in extreme levels of excitement. Less intense display may be reflected by partly erect combs, partly exposed cervical apteria, and partly raised and fanned tail, often accompanied by hooting. McNicholl (1978) described a number of variations of full and partial feather spread displays.

Fig. 15.15. Full feather spread display of *D.o. fuliginosus* male, Comox Burn, April 1975. Orange combs of this bird are transitional between yellow (normal) and bright red of birds in peak excitement. Photo by RJ Long.



A rare variant (in most populations) includes birds in flight with erect combs and fully exposed lateral cervical apteria. Such flights have been elicited by playbacks of male and female calls, retreat from an observer after having responded to a female dummy (McNicholl 1978), and females landing or cackling on or near territories. In 4 years of study at Comox Burn, McNicholl saw this display only eight times, but it may be more frequent in other populations. For example, on 24 and 25 May 1985, working with *D.o. sierrae* near Mt. Lassen, CA, we encountered seven singing males. Four of six that flew did so with exposed cervical apteria, all after having heard playbacks of female cackles. At least two landed on loud wing. Among four seen in flight on 11, 12, and 14 June and to which cackles were played, only one flew with exposed apteria. Birds there sing mainly from trees, songposts not generally available on clear-cuts. We do not recall having seen interior males fly with this display, nor have we heard it reported.

A male in full feather spread may move into a conspicuous position and sing or move toward an intruder or sounds of an intruder. He may make periodic stops to hoot as he moves ahead, or proceed without hooting. Once he detects another grouse, if a female, he may begin "display walking" (Hjorth 1970), a variation of feather spread in which the head and neck are lowered to nearly horizontal with the ground as he moves forward and with the head jerking back and forth with each step. He may stop, resume an upright stance, sing one canto, then resume the walk, occasionally bobbing his head up and down. When ≤6–7 m from the hen he may begin the "rush", a run, with head and neck near horizontal to the ground. The terminal phase of the rush usually involves a slight ±2 m curve toward the hen with primaries spread and wing tips dragging on the ground, producing a rustling sound. The tail is fully fanned and tilted toward the hen. On reaching her, a quick stop causes him to tip forward and is accompanied by a loud whoot. Hjorth provides fine details of this display. If the hen appears receptive, the male will attempt to mount her, but if she merely stands or starts to move away, he may begin the head bob phase of courtship display. He raises and lowers his head, with occasional up and down jerks. A rare addition includes pointing the neck, head, and beak skyward and jerking the head from side to side, sometimes referred to as "head darting" or "skypointing". In peak display and just prior to mounting the hen, the combs often flush with blood, changing from yellow, through orange, to bright red. Red may be retained for a short time only, for during copulation the combs often return to yellow. Although not timed, a change from yellow to red, or back again, may occur in a matter of <5 s. Unreceptive hens move off in neutral posture, often beginning the move with a short run. If rejected, a male usually resumes hooting, at first in full feather spread, but soon returns to routine hooting. If another hen is present, he may shift his attention to her while still in full feather spread. Hooting after departure of a hen supports the notion this is a signal to hens out of view.

Whooting is most often heard in the peak breeding period, clearly associated with courtship. Following peak breeding, about mid May in lowland Vancouver Island, there is a lull in whooting, likely a result of reduced frequency of encounters between males and females once most hens have begun to incubate. Whooting picks up again when chicks begin to hatch, for males court brood hens or those that have lost nests. By late June, whooting is seldom heard, likely a result of most hens not reacting to courtship advances because they have chicks, are incubating second clutches, or are through attempting to breed for the year. Males begin to abandon their territories. Although a few stay on territory and sing into early August, rarely early September, whooting is rare or non-existent in most of July—the latest record at Comox Burn was 5 August (McNicholl 1978). MA Degner recorded whooting at Hudson Bay Mt., where breeding is very late (Fig. 10.3), on 7 and 16 August, 1986, in both cases by males courting brood hens.

(h) *Copulation.* Our description of copulation comes mainly from aviary birds (Stirling and Bendell 1970), for this behaviour has rarely been observed in the wild.[18] A receptive hen squats and may whinny. Her yellow combs may be slightly brightened and enlarged but not to the same extent as in males. The male mounts her from behind, in full feather spread. He grabs her nape in his beak, drops his wings to her sides, with tips touching the ground,[19] and treads her back as he settles for coitus. Combs are yellow, reduced in size, and lateral cervical apteria are now only about half exposed. His back and rump feathers are raised and mostly closed tail depressed to the left (in all cases observed in the aviary), that of the female to the right. As he settles, the lower end of the oviduct of the female protrudes from her vent, and two copulatory papillae protrude from his. The papillae, upon which sperm are carried (Stirling 1965), and oviduct are applied to each other for 2–5 s (Stirling and Bendell 1970), accompanied by vertical tail beats of the male's tail (Hjorth 1970). Following coitus, the male releases his hold on the hen's nape and walks off over her head. In the aviary, both then ruffled their feathers for about 30 s. Males sometimes resumed full feather spread and began hooting, but often attacked the hen. Post-coital aggression also has been seen with dummy hens in the field.

Wild males readily court and attempt to copulate with dummy females and in one case with a freshly dead female that hit an overhead telephone line. In the aviary they may attempt to copulate with a crouched male. Males appear to be "coarsely wired", not as discriminating as females. Females are likely the sex involved in mate selection.

(i) *Agonistic behaviour.* Most adults occupy territories while on breeding range and defend them against other males (Bendell and Elliott 1967). If a resident sees or hears another grouse enter, or appear to be within, his space he investigates by moving toward the intruder. If the intruder is female, the resident may initiate courtship behaviour, but if a male, he may become aggressive. In either case, he often erupts into full or partial feather spread, likely signaling to a female, "here I am", to a male, "this space is occupied". If the intruder is male, the resident assumes a horizontal posture with feathers pressed tightly to the body (Fig. 15.16) and rushes at him in threat posture (Bendell and Elliott 1967). In most cases, intruders take flight, but if not, the resident may growl and pace back and forth in front of him, then attack, with the intruder taking flight or engaging in a fight. Such encounters usually result from nearby males following or approaching females across territorial boundaries. Males seem to know their own boundaries and those of their neighbors, which they seldom cross.

Fights are rarely seen or heard [they tend to be noisy from growling and buffeting of wings]. Bendell and Elliott (1967, p. 18) described a typical fight:

> ". . . both males pace in threat posture in tight ovals and give threat calls [growls]. They stop periodically and face each other with upstretched necks. They then return to threat posture and pacing. Suddenly they engage with vigorous pecking, buffeting of wings, and downward slashing of feet. . . . [they] may break and resume pacing and threatening. It seems that one bird tries to get above the other on the surrounding ground and from this position another engagement results."

Two such complete encounters were observed, lasting 5 and 25 min, respectively. In the first (5 min), one bird suddenly broke away, was pursued about 5 m, and disappeared. The victor withdrew about 30 m and began to hoot. In the second, there was only ~1 min of actual fighting. At end, when the birds were separated by a mound of earth and vegetation, each withdrew toward the centre of its own territory. Among 10 observed fights where territorial boundaries of both participants were known, all occurred on or near the boundaries. Hjorth (1970) reported, from observations of a male attacking

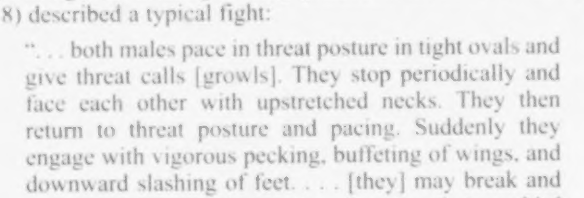


Fig. 15.16. Threat posture of male. Drawing by ChW Gronau.

a mounted dummy male, that the eye combs were sometimes bright red, sometimes bright yellow. "Blue grouse are long-lived, and a few fights, if any, may . . . space the birds for a number of breeding seasons" (Bendell and Elliott 1967, p. 18). Some males attack, and attempt to fight with, their own image in a mirror, suggesting they don't self identify.

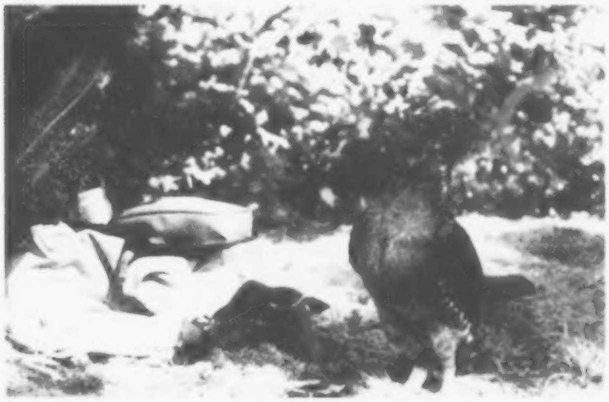
Most male:male aggression appears to occur at twilight, April through June, mainly in April (Stirling and Bendell 1970). In one year, 21 cases of male intrasexual aggression were noted on Vancouver Island, all between April and the end of June, even though singing continued into August. From this, Stirling and Bendell suggested (p. 169), ". . . aggressive display apparently ended in June, . . ." This contrasts with a possible increase in yearling male growling in late summer, but that is in response to human intruders, not other males, and likely involves the softer, slower variant of the growl.

Adult males often react to intrusions by observers with presumed agonistic behaviours. Some birds involved in routine hooting almost immediately erupt into full or partial feather spread on seeing an intruder or dog and continue to hoot in full view. This may be an attempt to advertise possession of space or intimidate. If pressed too closely, some shut down feather spread and walk off growling, with no clear display other than a folded and partly raised tail and raised crest. One cannot be certain these behaviours represent aggression, for they may reflect little more than an advertisement of occupied space or ambivalence, a combination of fight or flight. Rarely, a super aggressive male will stand its ground and attack an observer (Fig. 15.17).

Murie (1937) reported an incident near Norris, MT, where a male was attracted to his car, curiously circling it when the motor was running, but leaving it when the motor was stopped. It would return when the motor was started. It landed once on the hood of the car and twice on a fender. Murie thought this bird was confusing the sound of the motor for another grouse. This male was likely defending his space.

Males, and sometimes females, of several different species of grouse sometimes expose a patch of white feathers from under the wing, at the proximal end of the humerus, during interactions with other grouse, the so-called "shoulder-spot display" (Lumsden 1970). Its exposure has been variously interpreted as evidence of fear (Lumsden 1970; McNicholl 1978), subordinate (McNicholl 1978), and agonistic (Hjorth 1970; Lumsden 1970; McNicholl 1978; Jamieson 1983*b*) behaviours, always appearing in conflict situations. McNicholl reported it as associated with three different agonistic postures in blue grouse, although not always accompanying them; thus, not a necessary component of aggressive interactions. Perhaps it expresses a certain level of aggression or aggression specific toward certain individuals. He also found that males would court male dummies when accompanied by female calls, but would attack the same dummies with the same calls if artificial white spots were added. From this, he suggested that the shoulder spot is a strong releaser of aggression. Jamieson (1983) reviewed this topic for blue grouse and concluded that exposure of the shoulder spot was seen only in aggressors, especially in adult males when driving off yearling males. The bulk of evidence indicates it is most apparent in aggressors in conflict situations, at least in blue grouse.

Fig. 15.17. Territorial male about to attack boot of intruder, Kw'as Park, Cortes Island, BC. This stance is that of fighting males prior to pecking at each other or at their image in a mirror.



15.3 Hens and chicks

In spring, all females are broodless, but once the first clutch of eggs on an area hatches there are two clear classes on breeding range: hens with chicks, and lone, or broodless, hens. The latter includes nest hens as a distinct subgroup and which temporally overlap with brood hens. Since much juvenile behaviour is intimately related to that of their mothers and siblings, we consider juveniles along with hens.

15.3.1 Lone females, except nest hens

(a) *Sociality*. Females without brood are usually alone (Table 15.3). They are courted by territorial, in some cases non-territorial, males if detected, principally in early spring. If not receptive, hens tend to move away from males. They are seldom found with other females in spring or early summer. After mid July, two or three may be found in small groups. These birds appear to be failed, or non, breeders and are likely in initial stages of return to winter range.[20] Among 158 radio locations of 30 broodless hens at Comox Burn following loss of their nests or chicks, 80% were in or at the edge of conifer thickets (Sopuck and Zwickel 1992).

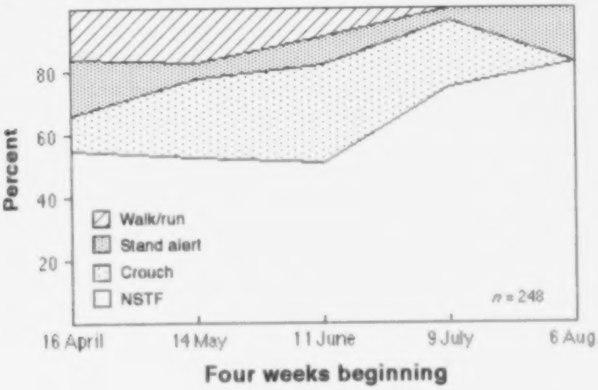
Lone females are most often flushed or found crouched when first seen (Fig. 15.18). In this sample, there was a tendency, not quite significant [9], for birds to flush more often as the season progressed. Ninety-six percent of all lone females

Table 15.3. Sociality of broodless females by 4-week periods at Comox Burn, 1971–1972.

4 weeks beginning	Alone[a]	With female	With male
16 April	74 (88%)	2	8
14 May	68 (97%)	0	2
11 June	26 (86%)	2	2
On or after 9 July	22 (81%)	4	1
Total	190 (90%)	8	13

[a] Birds were classified as alone if > 10 m from any other bird (females on nests were excluded from this analysis).

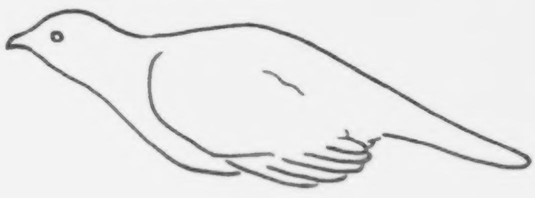
Fig. 15.18. Behaviours of lone females when first seen, by 4-week periods, Comox Burn, 1971 and 1972. NSTF, not seen till flushed.



flushed from, or were first seen on, the ground. Most that stood or moved away on the ground did so in alert posture, 20% with raised crests, a percentage that did not change throughout summer. These hens were more likely to cluck as summer progressed; 33% mid April to 8 July (88/266), 60% after 8 July (18/30) [10]. Among 55 lone hens sampled at random, mid April to mid June, 67% were silent, 18% gave soft, short, clucks (one or two notes only, the "hard cluck" of Stirling and Bendell 1970), and 15% longer, often louder, clucks (extended hard clucks), usually when in flight. This call appears to be an expression of apprehension or alarm.

(b) *Reproductive behaviour*. Some time between mid April and mid May is the period of peak breeding in most areas, but owing to the nature of our search, the dispersed territorial system of males, and the secretive behaviour of most females, breeding was rarely seen in the field. Stirling and Bendell (1970), however, described basic breeding behaviours of females in the aviary. They described one posture, "squatting", and two calls, the "whinny" and the "quaver cry", related to reproduction.

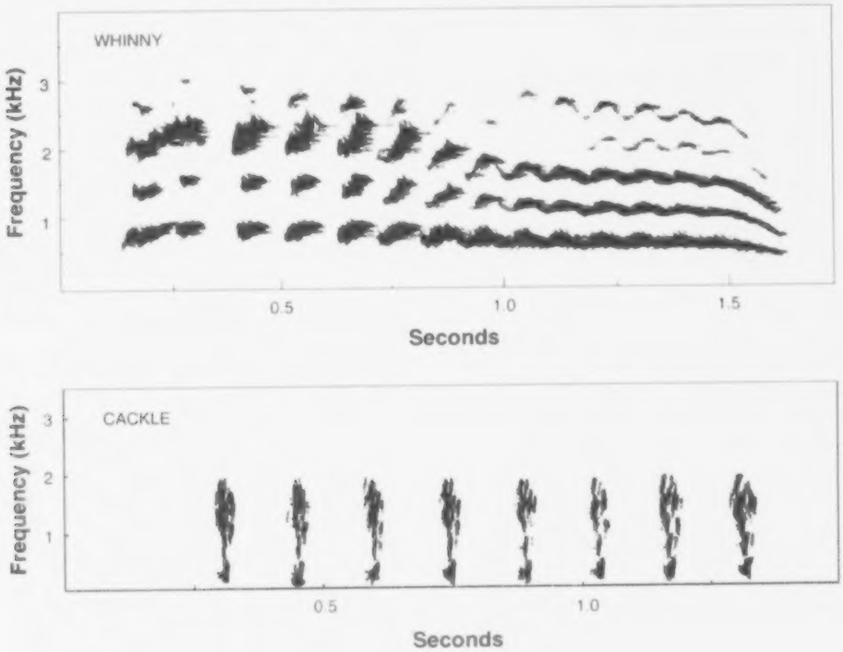
Fig. 15.19. Squatting posture, a female signifying readiness to copulate. Drawing by ChW Gronau.



Squatting (Fig. 15.19) is assumed by the hen for copulation and involves a crouch to the ground with neck and head elevated and tipped slightly forward. Wings are dropped to the sides, with primaries opened slightly. Combs, normally inconspicuous and slightly yellow, may become slightly enlarged and brighter yellow. Aviary birds squatted for only 3 days, a short period of "estrus", helping to explain why few copulations are observed in the field. In the aviary, Cooper (1977, p. 66) heard some sexually receptive hens give a raspy, guttural call he termed a "croak" [not reported in wild birds]. They often croaked immediately prior to squatting, in one case while laying an egg. See 15.2.3 for interactions with males during copulation.

The whinny (Fig. 15.20), so named because of its similarity to the first part of a whinny of a horse, was heard only in the squatting season, and was given by ~40% of 66 hens held

Fig. 15.20. Whinny and cackle calls of females. Recording and sonogram of whinny, *D.o. fuliginosus*, by I Stirling in aviary; of cackle by J Kristensen, at Comox Burn.



in the aviary (Stirling and Bendell 1966). It was postulated to be an inducement to the male to copulate and was rarely replied to by other hens. Aviary males responded by hooting and feather spread and playbacks of this call sometimes caused territorial males to sing.

Since the whinny was given just prior to copulation, Stirling and Bendell thought it might be the female counterpart of the male whoot. Variations of this call, the "attack whinny" and "whinny scream", have been reported in experiments in which wild hens were attracted to dummy females by playbacks of cackles (Bergerud and Butler 1985). Both whinny-like calls accompanied attacks on the dummies. As well, they have been heard from at least one agonistic nest hen (Hannon 1978) and brood hens (see 15.3.3(e)).[21] These apparent variants of the whinny may be different calls.

The quaver cry, now more commonly referred to as the "cackle" (Frandsen 1980; Hannon 1980; Hannon et al. 1982; Bergerud and Butler 1985; Fig. 15.20), was given by hens that squatted or laid eggs (in the aviary) and was sometimes given by hens when showing agonistic behaviour. In contrast to the whinny, the cackle often enticed other hens to return the call, and aviary males sometimes responded by hooting and feather spread.

Stirling and Bendell (1970) reported that the cackle was heard most often in the field in twilight hours, 0430–0530 h and 2130–2230 h, rarely at other times of day, and mainly during the period of peak copulation. They hypothesized that it may (1) indicate a readiness of females to mate, (2) synchronize male and female reproductive cycles, and (or) (3) warn other hens away, a mechanism involved in spacing behaviour. They thought this might be the female counterpart of the male hoot.

At Comox Burn, Hannon (1980) tested the above hypotheses. She concluded that hens that cackled were not necessarily receptive to males, casting doubt that it functions to attract males or synchronize male–female breeding cycles. Since females returned cackles of other females, Hannon felt it might advertise occupancy of an area and warn away other hens. Later studies indicated cackling increased as hens localized for nesting and that its peak coincided with the period when most females were localized, but not yet incubating (Hannon et al. 1982). Frequency declined as incubation began and ceased once all females were incubating.

Although female aggression is rarely observed, the cackle has been implicated in agonistic interactions between females in both natural (Lewis 1984*a*; pers. observ.) and experimental (Bergerud and Butler 1985) situations in the field. Hannon et al. (1982) and Bergerud and Butler both considered it a female:female aggressive call that may contribute to a dispersed pre-laying distribution of females, maintained by mutual avoidance rather than overt aggression.

(c) *Overt aggression among females.* Overt aggression between females has been observed in the aviary during pairing and mirror tests (Stirling and Bendell 1970), situations in which females cannot avoid other females or their own images. Hens paired together hopped into the air and struck down with the beak, with wings held loosely at their sides. In mirror tests, hens stood upright, stretched their necks, pecked downward at their images, and gave a "hard cluck" (a "bruck-duck" sound) that appeared to be a threat call. They were overtly aggressive only in April and May.

Bergerud and Butler (1985) conducted 10 tests on Stuart Island in which cackles were played to attract wild females to a set of mirrors by which a dummy female had been placed. Three answered playbacks by cackling and advanced to the "arena". One attacked its mirror image and the dummy, another only the dummy. Three instances of aggression between wild hens on Stuart Island were elicited by playbacks of the cackle, and five attacks on dummy females were seen on Vancouver Island.

Bergerud and Butler described attacks as "hesitant" or "hard". Hesitant attacks involved a slow advance, often a stop, cackling, and a "nee-uk" call (likely our "liquid cluck", see 15.3.2(d)); rectrices were sometimes fanned and the wing next to the dummy dragged. When near the dummy, cackles were replaced by attack whinnies or whinny screams. Assaults were usually brief and included an upward jump and downward blow with the wing and beak, then a jump away. Hard attacks involved a rapid advance with attack whinnies. Bodies were horizontal to the ground, plumage sleeked, necks extended, and tails closed. Blows to dummies were rapid and attacks extended, sometimes continuing until the playback ended. Among 10 belligerent female:female interactions, all were elicited by playbacks of the cackle. Whinnies sometimes attracted females to arenas, but none caused an attack.

All of the above interactions were elicited during experiments, and only a few unelicited (by observers) agonistic interactions by females have been seen. Bendell (1954) saw a hen persistently chase another in an open feeding area at Lower Quinsam on two consecutive mornings. Lewis (1984*a*) saw an aerial chase by one hen of another, from tree to tree on Hardwicke Island, with whinnying and cackling by both, but no physical contact. And on shrub-steppe range in the Methow Valley, four hens were observed feeding on newly emerging leaves in a small grove of black cottonwood (*Populus trichocarpa*); all within ~7 m of each other (pers. observ.). At least three cackled, up to three at one time. Intermittent cackling was mixed with intermittent feeding. One hen approached another to within ~1 m, was immediately chased off, and landed ~5 m away. Both then cackled. This observation and that by Bendell (above) suggest hens may use common feeding areas at the boundaries of, or perhaps outside of, spring "territories", engaging in agonistic interactions when a minimum individual distance is violated.

Small groups of 2–4 hens without chicks are sometimes seen on summer range (Wing et al. 1944; pers. observ.), although most are found singly (Table 15.3). Broodless hens thus tend to show exclusivity even in summer, but whether this is maintained by avoidance or exclusive use of space is not known. We suspect the former, and if true, there could be wide home range overlap with other broodless females, hens with broods, or males. Those found together may be initiating return to winter range.

15.3.2 Nest hens

(a) *Laying.* Little is known of the behaviour of laying hens in the wild because of their secretive behaviour and because laying birds cannot be readily told from those not laying. Two things we do know about laying hens is that they restrict their movements to a relatively small area in the vicinity of the nest site shortly before beginning to lay (see 17.3.2(b)), and the approximate rate of laying (see 10.4.4).

(b) *Incubation.* An incubating female's behaviour is critical to the production of new offspring. Hens that complete incubation spend ~7% of their annual cycle (26/365 days[22]) in this activity, with ≥95% of this time on the nest.

In most contacts with incubating females, she is aware of the observer. Caswell (1954*b*, p. 63) watched an incubating hen ". . . from a tree . . ." about 11 m from her nest. He presumably thought he had no effect on the hen and reported, ". . . the hen sits motionless except for an occasional movement of the head." This is the usual observation when one approaches a "sitting" hen (pers. observ.), but may reflect in part her reaction to disturbance.

The most comprehensive published descriptions of incubation behaviour are by Lance (1967, p. 24-25). He monitored four sitting hens with radio-telemetry, two of which were also watched.

> "Three of the four sat motionless on the nest, excepting just before they left to feed and just after they returned. At these times, the radio signal revealed they briefly shuffled about, perhaps adjusting themselves on the eggs . . . another distinctive radio signal revealed that the eggs were turned by the hen just after she returned from feeding."

> "Signals from the other hen revealed that she was in continuous motion while she incubated, even to the day of hatch. I could not approach her undetected, and doing so made her become still. The movement signal returned as I withdrew."

J Kristensen (pers. comm.) spent many hours watching incubating females from a blind at Comox Burn. Hens sat relatively still for long periods of time except when standing up to turn eggs or leave the nest. If airplanes or avian predators flew over, hens cocked their heads to "keep an eye" on the potential threat. If birds not in view vocalized, or in reaction to other sudden sounds, incubating hens stretched their heads and necks up high in an attempt to detect the source. Often ants and other insects crawled toward or into the nest or onto the bird. Hens pecked at these insects, either eating them or killing and discarding them. Clearly, incubation by most hens consists of long hours spent virtually motionless.

To the best of our knowledge, only one sound has been heard from relatively undisturbed sitting hens. Occasionally, when a nest is approached during late incubation and hatching, a very soft, almost inaudible, "tututu . . ." sound can be heard (Fig. 15.21), the "coo" of Kristensen (1973), who heard it from his blind[23] and first described it. It sounds somewhat like the purring of a cat, seems to carry no more than ~10 m, may be missed if not listened for, and has also been heard from hens with very small chicks. Because of its distinct notes, we refer to it as "purring" rather than the coo. Its fundamental frequency, at about 200 Hz, is the lowest frequency call we have recorded from females. This may be a contact call with chicks still in the egg (J Kristensen, pers. comm.), and to very young chicks. Contentment is suggested by its softness and similarity to purring. To our ears it sounds much like the "purring" of chicks as they settle for the night in an artificial brooder (see 15.3.3(d)).

(c) *Recess periods.* More attention has been devoted to recesses than to incubation behaviour, partly because of concern over the potential for cooling of the eggs or their exposure to predation. Lengths of recesses, their timing, and behaviour of the hen when departing from, and returning to, the nest have all been examined in greater or lesser detail.

Most early observations were fragmentary, involving notes as to whether hens were present or absent at nests, observations of hens leaving or returning to nests, and notes on their behaviour while away (e.g., Bendell 1954; Caswell 1954*b*). Among 34 nest visits in full daylight at Lower Quinsam, hens were absent six times (18%), and in 15 visits in early morning or evening, hens were absent nine times (60%) (Bendell 1954), a significant difference between daylight and crepuscular periods [11]. These data suggest regular evening and morning recesses. Bendell (p. 73) saw two hens make evening flights, one of which first made,

> ". . . soft quavering notes [purring?], then suddenly moved and took flight from the nest . . . She returned in 14 minutes from the same direction . . . in which she had flown. On arriving she landed with silent wings within a foot of the nest and . . . disappeared into the surrounding vegetation. Another hen [landed] silently within 20 feet of her nest at the completion of a morning and an evening flight."

Territorial males are attracted to flight sounds, and Bendell speculated that landing quietly might avoid such attraction.

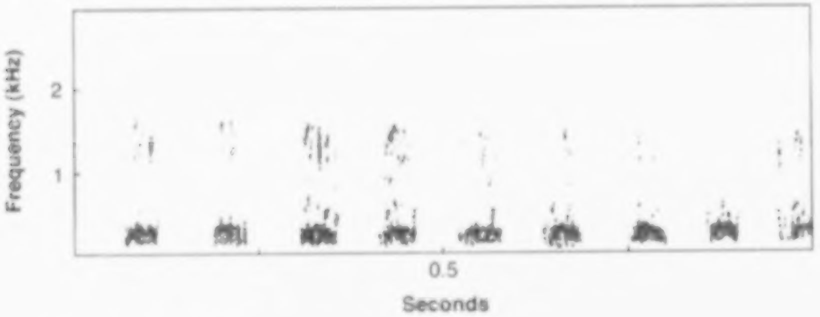


Fig. 15.21. Purr of nest hen, Comox Burn. Recording and sonogram by J Kristensen.

Flights of ~150 m were not uncommon. In sagebrush habitat in Idaho, nest hens flew 6–30 m, "just above the shrubs" (Caswell 1954*b*, p. 64).

On arrival in open feeding areas at Lower Quinsam, nest hens moved about completely exposed, feeding on "... almost everything vegetable. . ." (Bendell 1954, p. 74). During recesses, they preened, dusted, chased one another, and defecated. As many as three banded hens fed in one evening in one area, and one persistently chased another on two occasions. In all other cases they moved and fed independently of one another. Females feed voraciously when off the nest (Zwickel 1992).

"Clocker droppings" (see 12.4.3) are produced by incubating hens and are usually found some distance from the nest. Bendell (1954) watched hens defecate upon alighting, after flying from near the nest site during morning and evening recess periods. From this, and because clockers were most often found in open cover [most used for feeding], he suggested defecation takes place after the feeding area is reached. Caswell (1954*b*) noted that groups of clockers may be found in an area 3–5 m^2, indicating some hens may return to specific sites to begin recess activities. We, too, have seen such groups, but our observations indicate they are usually more widely dispersed, indicating they may be spaced. Following hatch, hens often leave a clocker very near the nest, occasionally in it, presumably as they and the brood depart.

An extensive examination of recess behaviour of a radio-marked yearling was provided by Lance (1967). Ten feeding sites were used, and the hen most often flew to them from near the nest, returning in the same manner. She usually walked 1–2 m from the nest, paused, and surveyed her surroundings before taking flight. She sometimes returned by wing, landed, and surveyed the area before walking onto the nest. One feeding site was reached by walking, with a return by flying, but at another, she walked both ways. This hen took recesses during all evening observation periods but that of the night before leaving the nest with her chicks, and in four of six morning observation periods. Modes of travel were most consistent for evening recesses; she flew to and from the nest in all but one case. She usually walked one or both ways in the morning. Flying from near, or to, the nest area seems most prudent, leaving less of a scent trail that might attract mammalian predators.

Lengths of recesses varied from 7 to 60 min (usually 7–10 min) with no clear relationship between weather and length. The longest was on a cool overcast evening and the shorter were often on warm, clear evenings. Recesses began 20–45 min earlier on overcast than clear evenings. Rate and intensity of feeding did not appear to vary with supposed quality of site (dry or mesic), even though longer feeding might be expected at dry sites [fewer succulents]. For other information on lengths and numbers of recesses see 10.5.3.

Some birds cover their eggs when they leave the nest (Bennett 1938; Hochbaum 1944), but this is rare in blue grouse. Among many checks of nests when hens were absent, we have only three records of eggs being covered, one each at Middle Quinsam, Comox Burn, and Hudson Bay Mt.; all clutches were in the laying stage. At Middle Quinsam, the eggs were covered with ~2.5 cm of dried leaves, at Comox Burn they were partly covered with fir needles, and at Hudson Bay Mt., partly with litter (kind unspecified in field notes).

(d) *Nest defence/display*. Caswell (1954*b*, p. 64) reported, "birds flushed from nests did not ordinarily make a sound or feign injury", and Bendell and Elliott (1967, p. 48) saw "no particular display . . . that may be related to defence of her nest or the distraction of an intruder from it." We now know, with larger samples and more observations, some hens defend their nests vigorously, even from humans.

Most incubating females sit very tightly, and some must at times be pushed off the nest physically to count or check their eggs. Most must be approached more closely than 2–3 m before being flushed by an observer or dog.[24] Sitting tightly might be considered covert, or passive, nest defence. Beyond that, we and our co-workers have recorded the following overt behaviours that are clearly, or appear, related to nest defence: "puff up" breast feathers, which makes the bird appear larger; "ruff up" neck feathers; erect and (or) fan tail; erect crest feathers; lower and drag wings, at times with alulae extended; flutter wings; fly at and strike an observer; peck at objects or hands extended toward them; hiss; and cluck (perhaps the hard cluck of Stirling and Bendell 1970). Hens might react to an intruder with only one of the above or with two or more.

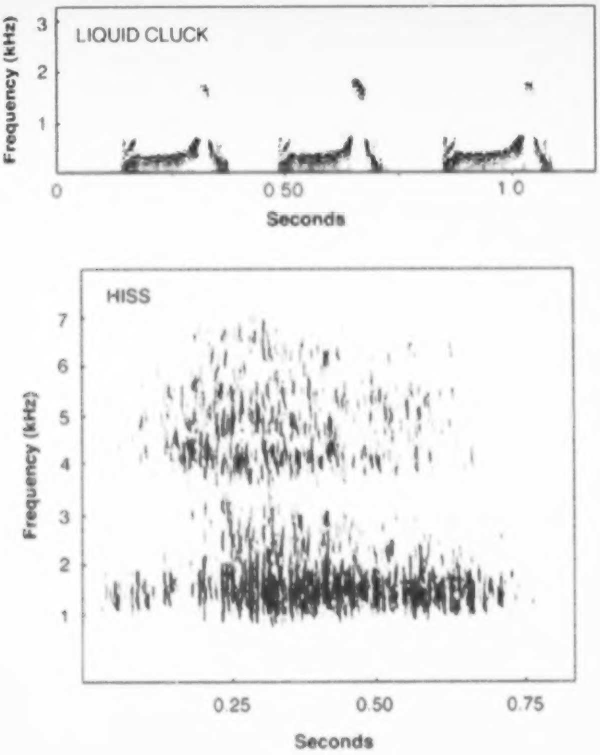
We often checked active nests to determine their status. Occasionally, hens were flushed or forced off nests to check the eggs. We examined 95 nest records (1971–1975) at Comox Burn for evidence of behaviours listed above.

One measure of a hen's reaction to disturbance is how tightly she sits. Among these 95 birds, 7 did not leave the nest even when touched by the butt of a noosing pole, a hand, or some other object during at least one attempt to flush them, and in these cases observers withdrew. Among 18 that left the nest when touched, 9 elicited no overt behaviours and 9 reacted with one or more, often after having stepped off the nest or flushed 2–3 m away. Nine others reacted with one or more displays or sounds after flushing without being touched, usually by having an object or hand extended very close to them. Thus, at least 18 (19%) behaved aggressively toward an observer, with 7 refusing to leave the nest even when touched. In total, at least 34 (36%) exhibited some form of aggression, refused to leave the nest when touched, or had to be touched before leaving the nest. Among 18 that reacted aggressively, 7 elicited at least one listed behaviour (weak responses), 4 elicited two (moderate responses), and 7 elicited three or more (strong responses). Since some observers did not record behaviours, or did so minimally,[25] and some hens were never forced off the nest, these are minimal figures for these hens.

We performed a similar analysis for 5 hens at our Duck Creek study area, 2 at the May Ranch, 14 at Skalkaho, and 2 at Hudson Bay Mt., a total of 23. Among these birds, eight left their nests after being touched, four without display and four with display, and two flushed without touching, then displayed. Among six that displayed, two elicited weak, one moderate, and three strong responses. In total, 10 (43%) exhibited some form of overt behaviour or had to be touched before leaving the nest. At least one at each area exhibited some form of defence or display. Collectively, these results were essentially the same as for birds at Comox Burn.

(e) *Experimental evidence for nest defence*. Further evidence for nest defence was provided in experiments conducted by Hannon (1978). She performed three types of experiments with five females: (1) presentation of a mounted female dummy on the end of a long pole to a sitting hen, or placement of a dummy at the nest during a recess; (2) presentation of a small cardboard box on the end of a pole to a sitting hen, con-

Fig. 15.22. Liquid cluck and hiss of females. Recording and sonogram of liquid cluck by J Kristensen, Comox Burn; hiss recorded by FH Backhouse, Hardwicke Island, sonogram by D Albright.



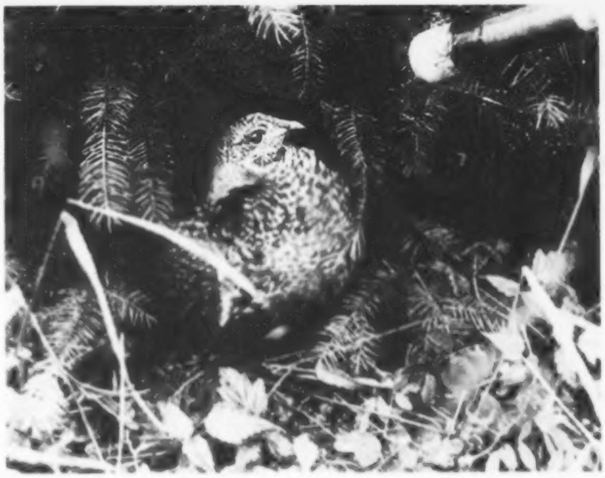
sidered as a control; and (3) placement of a live female inside a small plexiglass arena near the nest with the hen present, or during a recess.[26]

Among 13 experiments, hens reacted overtly in 11, ranging from jumping or flushing from the nest to attacking a dummy or the arena. Among these, sjx clucked, three "liquid clucked" (see below), one hissed, and one "soft whinnied" (Hannon 1978). Clucking may express alarm rather than aggression, but since it sometimes accompanied overt behaviours that were clearly agonistic (e.g., hissing and drooping of wings), it likely has an aggressive component in some situations.[27] In five cases hens showed very clear aggressive behaviour toward the stimuli presented to them.

The liquid cluck (Fig. 15.22), sometimes described as "yuk" or "gyuk", was first heard in our aviary, given by a hen laying an egg. It was reported in the field as given by incubating hens near time of hatch, or on their return to nests at which dummy females had been placed in their absence (J Kristensen, pers. comm.). This call has been heard as early as 8–9 days into incubation and was given by one hen that jumped off her nest and attacked a dummy. The whinny given by one nest hen was clearly agonistic. Judging from the sonogram of the "nee-uk" call reported by Bergerud and Butler (1985), it appears to be our liquid cluck.

Thus, clucking, hissing (Fig. 15.22), the liquid cluck, and the whinny may all accompany other agonistic behaviours by nest hens. All experimental regimes to which Hannon's (1978) hens were exposed, including the box, elicited defence behaviour in some cases. We conclude from observations during nest checks and from Hannon's experiments that some hens defend their nests, whether covertly (sitting tightly), or by a range of agonistic behaviours that may entail physical attack of the intruder. Degree of defence, however, varies among individuals. Some hens leave nests readily—others must be driven off (Fig. 15.23), even physically removed. It is our impression that individuals that readily leave nests and move away, or are aggressive, tend to retain that trait throughout incubation; i.e., they do not become noticeably more, or less, aggressive as incubation progresses. We also see no evidence that nest defence differs between yearlings and adults, for among 25 showing aggression and for which we knew ages,[28] 41% were yearlings, the approximate percentage of yearlings found in most coastal blue grouse populations on breeding range (see Table 18.10).

Fig. 15.23. Aggressive nest hen about to peck at end of noosing pole. One egg is visible under breast feathers, Comox Burn, 17 June 1973.

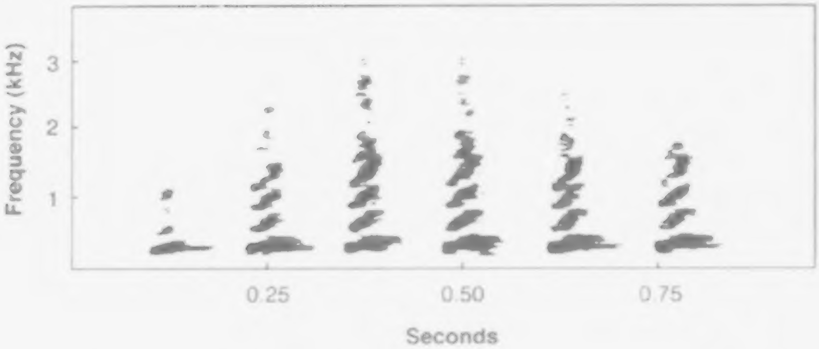


Field notes from two nest visits illustrate the tenacity of some hens:

Yearling female, Comox Burn, day 25 of incubation: "She stays on nest and pecks viciously at the [noosing] pole.. . . hisses and puffs her breast feathers to make herself 1/2 as wide again. . . clucked in response to chick whistle. When we pushed her off the nest she hissed, tail at 90°, neck ruffed, wings drooping, crest raised . . . walked around the nest . . . she went about 20 m from the nest and sat until we left." Two of four eggs were in pip stage at time of this visit. This hen also was strongly agonistic on day 4 of incubation, when the nest was found, and during checks on days 6, 18, and 23.

Adult female, the May Ranch, day 23 of incubation: "She flushed off [nest] clucking when Mark's hand . . . [was] ~10 cm from her. She ran around clucking and hissing, tail fanned and wings dragging. She flies at Mark . . . [as he was] checking eggs. She hit him on the back and legs. . . . stayed within 3 m of nest clucking while we checked eggs . . . We backed off 4 m and she returned to nest, standing on eggs clucking till we left." This hen also was strongly agonistic on day 12, when the nest was found, and during checks on days 14, 16, and 21.

Fig. 15.24. Clucking of a hen on return to a newly hatched brood in the nest. Hardwicke Island. Recording by FH Backhouse, sonogram by D Albright.



In short, yearlings and adults may defend nests, and may defend them virtually anytime during incubation. Although our samples are small from areas other than Comox Burn, this behaviour occurs across populations and subspecies. Defence behaviour, however, varies among individuals.

As noted above, when disturbed from a nest some females do not leave the immediate vicinity, but others may flush wildly and out of sight. If the disturbance abates and an observer hides, hens are usually back on the nest within a few minutes. If chicks have hatched and are still in the nest, hens may return to the nest and cluck very softly (Fig. 15.24), apparently "talking" to the chicks.

15.3.3 The female and her brood

Once with chicks, the behaviour of females changes dramatically. An elaborate system of vocalizations is apparent, in both hens and young. Many behaviours are reactions to, or with, each other, while others reflect reactions to disturbance. Both change as the young develop and maternal concerns wane. Almost certainly some are innate, others learned.

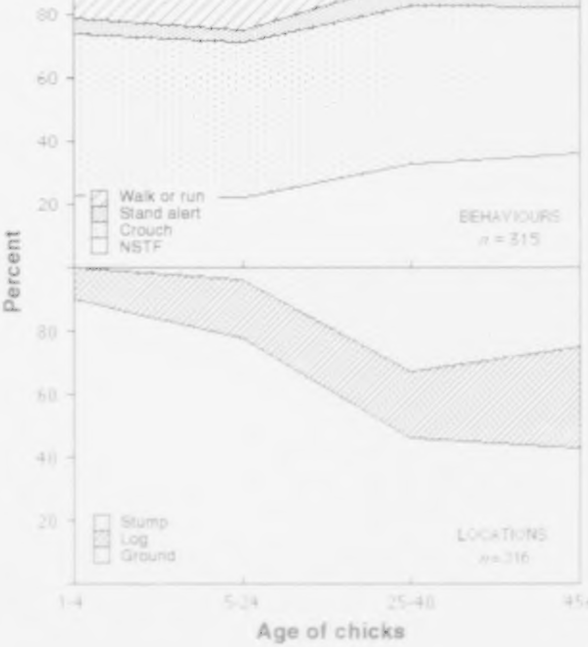
(a) *General behaviour of hens.* Unlike lone females, brood hens tend to hold their ground when approached, either walking slowly, standing alert, or crouching (and (or) brooding) when first seen by us (Fig. 15.25). If pressed, they often begin distraction display (see 15.3.3(f)), especially if with young chicks, but as chicks grow older, the hens more often flush.

At Comox Burn, hens were most often found on the ground when with young chicks, but were more often on logs or stumps as chicks grew older (Appendix 3 of Kristensen 1973; pers. observ.). At the Brownlee study area, brood hens sometimes acted as "sentinels" from the top of sage or bitterbrush plants (Caswell 1954*b*). Among 139 radio locations of brood hens at Comox Burn in late summer, only 24% were in or near thickets, significantly fewer than lone females, 80% (Sopuck and Zwickel 1992). Increased height and use of more open areas must give better surveillance, control of the brood, and detection of potential predators. On approach of an intruder, a hen positioned as a sentinel may crouch, stand alert and cluck, hop to the ground and attempt to lead the brood away, or flush. If pressed too closely, many begin distraction display.

(b) *Pre-hatch vocalizations of chicks.* The first vocalization of chicks of which we are aware is very soft peeping from within the egg, shortly before hatching and heard by placing the egg to the ear. It can be silenced by a sudden noise or shaking of the egg. No work has been done on this sound, but perhaps it helps to synchronize hatching, as proposed for "clicking" of embryos in eggs of bobwhite quail (*Colinus virginianus*) (Vince 1964), or communicates to the hen that hatching is near? The early stage of pipping, chipping at the shell with the egg-tooth, also can be heard by holding the egg to the ear, prior to when the shell is broken through.

(c) *Departure from the nest.* After all chicks are hatched, the female and young may stay on the nest for anywhere from ~6 to ~24 h, presumably allowing the chicks to dry and gain strength. Once dry and during this time, chicks may poke their

Fig. 15.25. Behaviours and locations of brood females when first seen, by age of chicks (days). Comox Burn, 1971 and 1972. NSTF, not seen till flushed.



heads out from under the hen or above her wings, make soft peeping sounds (similar to those while in the egg) and make short forays away from the nest, appearing rather clumsy. They may flap their wings on this first day. This is likely a time when chicks imprint on their mother and her calls. Much of the behaviour of hens with chicks now involves interactions between the two, a relationship that lasts into late summer or autumn in most cases.

Our observations suggest the brood usually leaves the nest sometime in the morning of the day following completion of hatch, occasionally in the afternoon, rarely in the evening.[29] A radio-marked hen at Comox Burn took no recesses in her last day on the nest (Lance 1967). Perhaps females forego feeding at this time so chicks do not stray during their absence? A long period with no recess likely explains the relatively common deposition of a clocker dropping in or near the nest at time of final departure. We do not know whether females or chicks initiate departure from the nest, but once away they virtually never return. In the first few days of life, activities of the chicks are mostly divided between brooding and feeding.

(d) *Brooding*. Newly hatched chicks have limited thermoregulatory abilities and are periodically brooded, usually on bare ground. Brooding refers to a hen keeping chicks warm, under her breast feathers and wings. This behaviour has been described in some detail elsewhere (Zwickel 1967*a*), and we summarize it here.

If chicks "wail" (see below), presumably in response to cooling, hens give a soft purring call, similar to, but louder than, that given while incubating. They settle to the ground, fluff their feathers, cup their wings, and purr until all chicks are under them. Hens also may be elicited to brood by a chick running under her, with no calls apparent. Occasionally, a female initiates brooding by settling into the appropriate position and purring, with no apparent elicitation from chicks, all of which usually return to her within 2–3 min. In the aviary, chicks seek warmth in an artificial brooder without stimuli from a hen.

Hens remain motionless and quiet during most of the brooding period but may shift position and purr, perhaps in response to activity under them. They often purr, and chicks often peep or poke their heads out between her wing and body, just prior to termination of brooding. One or more chicks may leave her and feed while she broods others. She usually stops brooding within 2 min or less of the first one to leave, but chicks sometimes return to brooding before cessation. At times, females merely stand and move off, with the chicks momentarily huddled in a tight ball before following her.

The ability to thermoregulate develops rapidly, and most daylight brooding ends by the time chicks are 10 days of age (Zwickel 1992; and see 11.4). In the aviary, young chicks give a soft purring call, a soft tutututu (Fig. 15.26) at start of roosting inside a heated brooder, but this has not been documented in the field. It develops into a soft puk-puk-puk in early weeks of life. The purr sounds similar to that of nest hens to us but has two clear harmonics lacking in that of hens. As well, that of chicks has a fundamental frequency of ~800 Hz with that of hens ~200 Hz (Fig. 15.21).

Two broods of young chicks, 1–2 days of age and 5–7 days of age, respectively, were each monitored on 2 consecutive days at Comox Burn (Zwickel 1967*b*). The first day was "cold" (and wet) and the second "warm" (with little rain), in each case. On cold days chicks brooded for ~80%–90% of the observation time; on warm days, ~50%. Feeding bouts decreased, and brooding bouts increased in length on cold versus warm days. There was no apparent relationship between when a hen started or ended brooding bouts and the occurrence of rain. No effects of reduced temperatures or lengths of feeding bouts on these chicks were detected. Distances between

Fig. 15.26. Purr and puk-puk calls of aviary chicks. Recordings and sonograms by Ian Stirling.

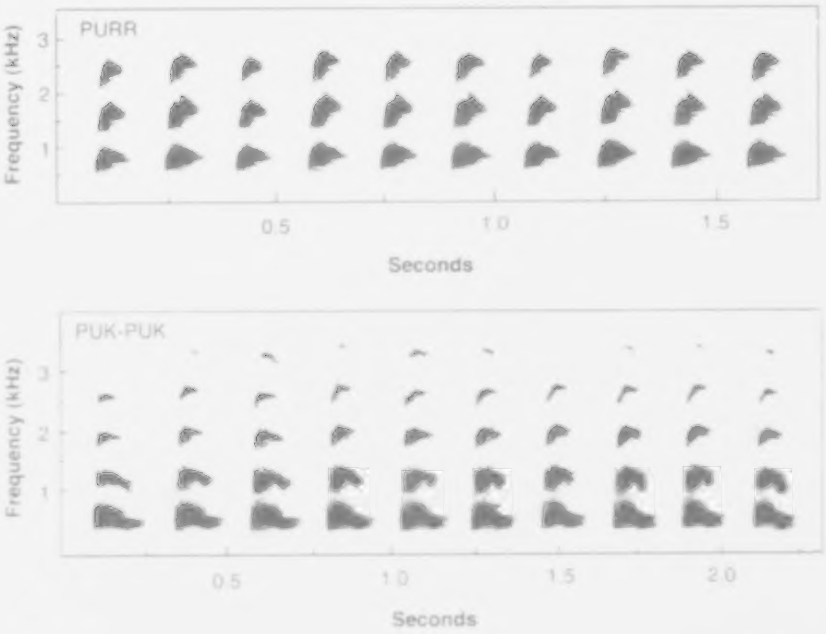


Fig. 15.27. Distances moved between brooding sites by two females, in percent by 10-m intervals. Data for females combined.

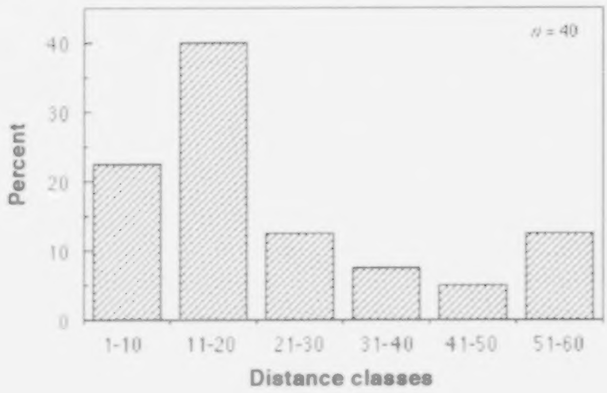
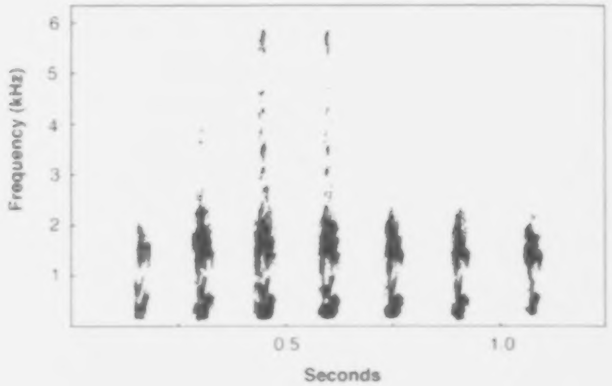


Fig. 15.29. Solid cluck of a brood hen, Comox Burn. Recording and sonogram by J Kristensen.



brooding sites of these two families did not differ, with an overall median of 18 m (mean = 24 ± 2.7 m, range = 1–61 m, n = 40).[30] Rates of travel did not differ between broods or among days, with a mean of ~2 m/min. More than 60% of all moves were <20 m (Fig. 15.27), only one <5 m.

(e) *Non-brooding*. Small chicks are somewhat clumsy for 1–2 days after leaving the nest but by 3 days are steady on their feet. When not brooding, they spend most of their time feeding and are a special case in terms of feeding behaviour (see 12.1.1). On clear days, they may sunbathe for short periods between bouts of feeding. When moving and undisturbed, they scatter around the hen, ahead, behind, or to her sides. Very young chicks tend to stay within ~5 m of their mother, but by a week of age they venture out to ~15 m, eventually to 30 m or more.

Aviary chicks flap their wings and make small "flight-jumps" when only a few days old (Cooper 1977, p. 47). By 6–7 days of age, wild chicks make short "hopflights of about 2 m" (Zwickel 1967*a*, p. 4). At 8–9 days they can fly 10–15 m, and at 2 weeks, 30–60 m.

Hens tend to feed nonchalantly when leading broods but maintain an alert attitude toward disturbance. Interspersed with feeding, those with very young chicks keep up a near-continuous and soft purring sound (perhaps an extension of the late incubation purring of nest hens) to which the chicks presumably cue, helping to maintain the integrity of the brood. Small chicks maintain a near-continuous soft peeping or "weep call" while feeding and which appears to express contentment. If a chick strays too far from the hen, perhaps out of range of her purring or weeps of broodmates, it may give louder and higher pitched "whee-u" calls and with even greater anxiety, may "wail" (Fig. 15.28). Wailing of small chicks is high pitched and whistlelike but decreases in pitch, increases in volume, and takes on a vibrato at ~3–4 weeks of age, by which time the weep and puk-puk calls have ended.

With increasing anxiety, wailing may become louder and can be heard for up to ~400 m under favourable topographic and weather conditions. If birds have been separated by a disturbance that has not abated, hens may cluck, the "solid cluck" of Kristensen (Fig. 15.29), and which silences the chicks. Its intensity varies among hens and situations. This appears to be a general warning[31] and sounds similar to the hard cluck of Stirling and Bendell (1970) to our ears. It produces, however, a spectrogram more like that of the cackle, but with harmonics not apparent in that call. If not separated, or a disturbance has abated, hens may begin a "tau-tau call" (see below) and chicks in question come running, at least until they are again within the group, and may resume feeding. At ~4 weeks of age, young birds sometimes give short "chirps", often seem gawky and curious, and may slowly walk away from observers, flushing or running if approached too closely (in "wild" popula-

Fig. 15.28. Wail call of aviary chick. Recording and sonogram by Ian Stirling.

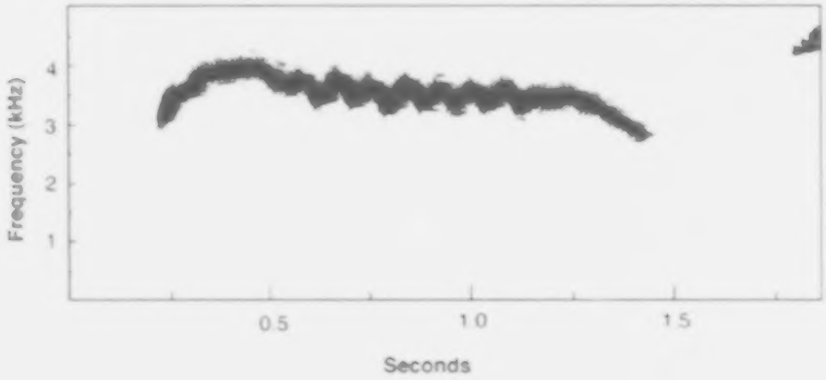
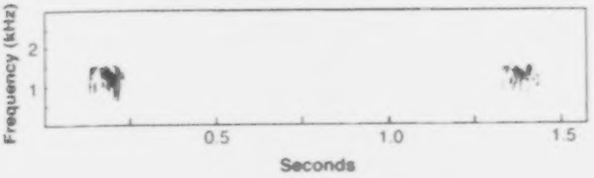


Fig. 15.30. Tau-tau call of a brood hen, Comox Burn. Recording and sonogram by J Kristensen.



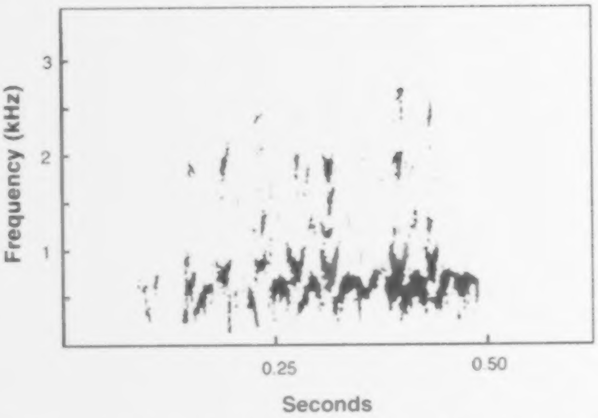
tions individuals tend to crouch, freeze, then flush, with few or no vocalizations). By 8–10 weeks, wailing ends, and chicks approached by an observer may give short cluck-like sounds. Wing et al. (1944, p. 436) thought wailing a call of "lost" birds, with which we agree.

After disturbance and scattering of hens and chicks, broods begin to reassemble rather quickly, usually within 10 min or less if the disturbance abates. Both tend to return to the site of disturbance. The hen returns, usually on foot, either on her own or in response to wailing of chicks. If chicks are quiet, hens may return silently and when at or near the area of disturbance, begin the tau-tau call (Fig. 15.30; the "tau-tau-tau" of Bendell 1954, p. 83; and "gaw-gaw-gaw" of Kristensen 1973, p. 27). It starts off loudly, fades toward the end, and brings chicks running or walking toward her. Hens also may give this call as they stand or walk in an alert posture toward wailing chicks, which stop calling and approach her. Rarely, a whinny-like call (Fig. 15.31) has been heard in conjunction with the tau-tau from hens reassembling their broods (Kristensen 1973; Albright 1984; Zwickel 1992).

Kristensen (1973) described a "warble cluck" (Fig. 15.32) that he described as a short garglelike sound. It and the solid cluck (Fig. 15.29), a harder and sharper sound, were given by some hens in response to wailing of chicks. The warble cluck initiated the clucking and, if wailing persisted, was followed by the louder solid cluck. He interpreted these calls as an attempt to quiet chicks when danger was present.

Even following release of a hen after banding, an extreme disturbance, many return to the brood area within 15–20 min, some within 10 min or less. Wailing tends to bring them back more quickly. If an observer sits quietly and out of sight, chicks soon begin wailing. Some hens sneak back quietly, others may walk or run, clucking loudly or giving a high-pitched "kweer-kweer-kweer" (Zwickel 1967*a*)—perhaps an extreme warning to the chicks. Occasionally, a hen will stay away up to ±1 h, with chicks reassembling as a group in the vicinity of where first disturbed, and wailing loudly. Some hens fly back and, on landing, give a high-pitched "kwa-kwa-kwa", appearing more solicitous of the brood than usual. This call may ask "where are you?", for chicks sometimes respond by wailing, even from inside a cloth sack (Zwickel 1967*a*).

Fig. 15.32. Warble cluck of a brood hen, Comox Burn. Recording and sonogram by J Kristensen.



Two observations of chicks in our aviary relate to the development of aggression, observations difficult to obtain in the field. Obvious aggressive behaviour, pecking at other chicks, has been seen as early as 3 weeks of age. And, in September, at perhaps 10–12 weeks of age, the first growling (presumably aggressive) of young males has been heard.

(f) *Distraction display*. Distraction display is behaviour by a female in response to perceived danger from a predator. It may draw attention away from the brood, which then has an opportunity to hide or escape. According to Armstrong (1947, p. 99), it ". . . is the product of two clashing motivations, . . . threat and escape." A number of authors have discussed distraction display, or brood defence, in blue grouse (Schottelius 1951*a*; Bendell 1954; Caswell 1954*b*; Henderson 1960; Bendell and Elliott 1967; Kristensen 1973). It has two basic elements, ". . . an attempt by the female to lead us away, and an intimidating rush toward us" (Mossop 1988, p. 17). Kristensen (1973), at Comox Burn, provided the most comprehensive analysis of this behaviour in blue grouse, and we use mainly his work to describe it.

Brood defence involves display and vocalizations. The first reaction of a female with very young chicks to a presumed predator is often to settle into a low crouch, at times with soft clucking. This clucking is likely a warning to the chicks, which may crouch or seek nearby cover. Those <4 days of age, still flightless, might "freeze" in place, but often scatter 3–4 m

Fig. 15.31. Whinny-like call of a brood hen, Comox Burn. Recording and sonogram by J Kristensen.

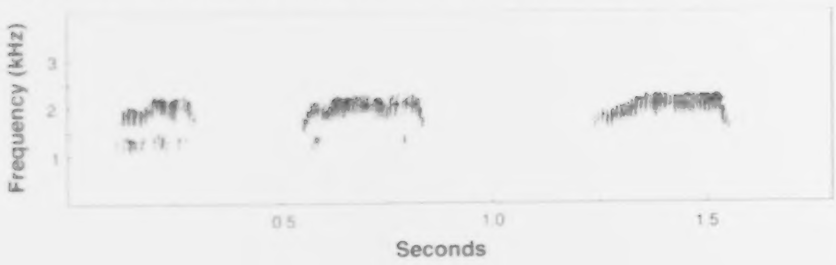
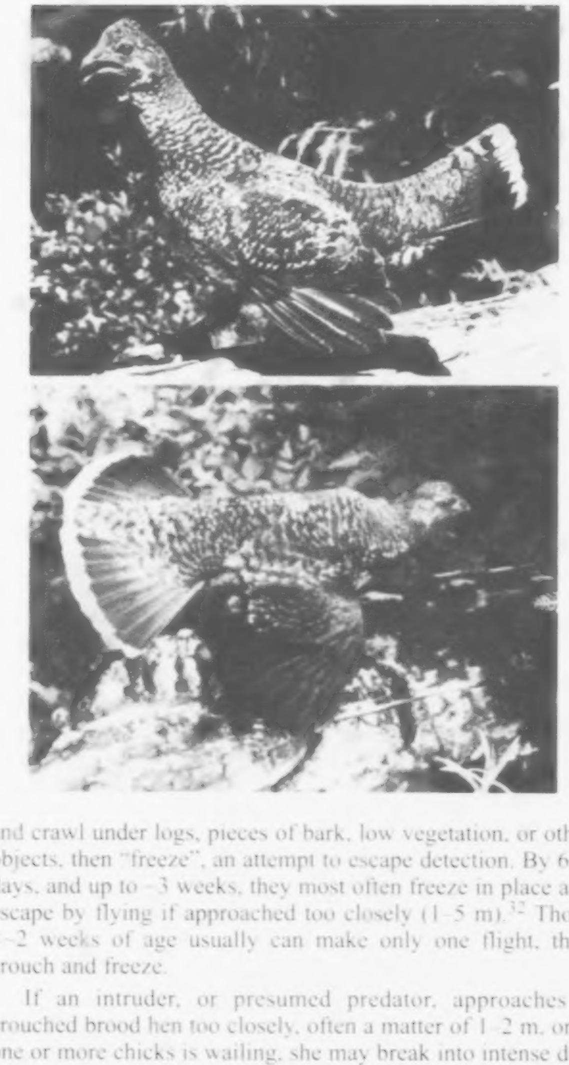


Fig. 15.33. Distraction displays of two brood hens: at Comox Burn (*top*) and at Lower Quinsam (*bottom*). Note that the upper female has a raised crest and partly raised and fanned tail, the lower female a fully fanned but unraised tail. There are numerous variations in distraction display.



and crawl under logs, pieces of bark, low vegetation, or other objects, then "freeze", an attempt to escape detection. By 6–7 days, and up to ~3 weeks, they most often freeze in place and escape by flying if approached too closely (1–5 m).[32] Those <~2 weeks of age usually can make only one flight, then crouch and freeze.

If an intruder, or presumed predator, approaches a crouched brood hen too closely, often a matter of 1–2 m, or if one or more chicks is wailing, she may break into intense display, clucking loudly. At full height, she may run around the intruder with neck,[33] breast, and other body feathers fluffed, crest raised,[34] tail erect and fanned,[35] and wings drooped or dragging on the ground,[36] or various combinations of these behaviours (Fig. 15.33). Other hens may run around the intruder in a horizontal crouch with wings drooped and (or) dragging. A very aggressive hen at peak display may hiss and virtually all will cluck (the solid cluck, Fig. 15.29).

Hens, especially those with younger chicks, sometimes fly at an intruder with exaggerated wing beats and loud clucking and (or) hissing. When close to the observer, the bird will flare, or stall, then land a short distance away, still clucking.[37] Some may make short hops off the ground, with or without wings flapping and accompanied by vigorous clucking. Others may attempt to lead the intruder away with short flights (and exaggerated wing beats) for a few metres, then glide a few metres, repeating this sequence as they move off.[38] Such "leading" also may involve running off with both wings drooped or dragging. Rarely, a crouched hen very close to an intruder and with very young chicks may quiver her outstretched wings (J Kristensen 1973; pers. observ.). Leading, wing dragging, and wing quivering have sometimes been likened to injury-feigning.

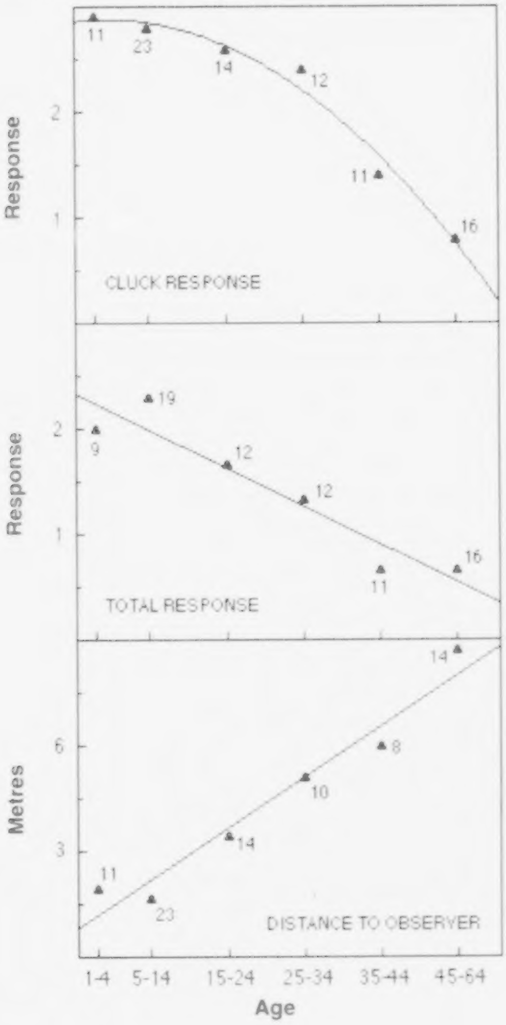
Distraction display most often lasts for only 2–3 min but may be more prolonged with especially aggressive hens, or if an observer simulates, or uses playbacks of, calls of chicks. On coastal clear-cuts, hens more often performed distraction display on logs and stumps than on the ground (J Kristensen, pers. comm.). After peak display, hens usually move off 15–30 m and may stand alert, clucking, or crouch silently. They often fly into a nearby tree if available. If not, they tend to settle on a high spot; often on a stump or small knoll on coastal clear-cuts, likely for better surveillance. Simulated chick calls will bring some hens back to their original location, usually clucking, and at times with a return to distraction display, but not as strongly as at first contact. Clucking by one brood hen, or loud calling by chicks, may cause nearby brood hens to cluck and move toward the disturbance, but they do not normally come in all the way.

With increasing age of chicks, distraction display wanes. Kristensen (1973) rated intensities of some distraction behaviours against age of chicks, and all were negatively correlated with age. Tail spread, wing droop, hiss, and flight at intruders tended to wane rather rapidly, beginning ~2 weeks after hatch. Clucking (Fig. 15.34) [12a] and raised crests tended to remain at relatively high levels for 3–4 weeks. Mean total response ratings[39] illustrate the general picture (Fig. 15.34) [12b]. In contrast to strength of displays, minimum distances from the observer during distraction display were positively correlated with age of chicks, beginning to increase ~2 weeks after hatch (Fig. 15.34) [12c]. By 9 weeks, many hens fly or run off silently, or with only mild clucking. If accompanied by loud clucking, distraction display sometimes attracts nearby males, which may begin hooting, or nearby brood hens, which may also cluck.[40]

Occasionally, when an observer comes upon a hen with very young chicks, often brooding, she breaks from a crouch or brooding position with a loud "scree", a high-pitched scream, and the chicks scatter. This is uncommon and seems to occur in situations in which the hen was not aware of the intruder until almost upon her (likely rare). We interpret this as an intense alarm call, and it is typically followed by intense solid clucking and display, although intensity varies among and within populations.

(g) *Summary of female and chick vocalizations.* Females have a much larger vocal repertoire than males, particularly when breeding and raising young. We have identified at least 14 calls in the field that appear to be distinct (Table 15.4) on the basis of both spectrograms and contexts in which they occur. As well, whinny-like calls have been reported (Bergerud and Butler 1985) that may be variations of the whinny, or different calls. Calls from the aviary that have been heard in the wild show no clear conflicts with interpretations of function from wild birds. The main difference is that the circumstances in

Fig. 15.34. Mean clucking responses, mean total responses, and mean minimum distances of brood hens to observers during distraction display, all relative to age of chicks (in days), Comox Burn, 1971. Data extrapolated from Figs. 6, 10, and 8 of Kristensen (1973), respectively. Numbers are sample sizes.



which many have been heard in the field is greater than can occur in an aviary. Besides calls above are seven other sounds reported only from aviary females[40] and which we have not attempted to interpret here. These bring the potential number of identifiable female calls to well over 20, and we suspect more.

Calls of females are not always easy to differentiate, for they sometimes occur in different combinations, blend together, and vary in length and loudness. They may sound very similar to us, yet produce different spectrograms, be given in very different situations, and convey different messages. Some may be determinate, always having the same number of notes or lengths of phrase, e.g., the whinny. Others may be indeterminate, given in short or extended phrases, e.g., hard and solid clucks. Some may always be given at about the same volume, e.g., the cackle and whinny, others may vary from soft to loud, e.g., hard and solid clucks. Confounding differentiation is that hearing differs among observers, resulting in different terminologies and interpretations. Nevertheless, we are confident that all in Table 15.4 are sufficiently distinct to be considered as different calls. Female vocalizations, especially, need further research, both within and among local populations and subspecies.

Associated with development, calls of chicks change in their first summer. For example, the weep of small chicks grades into and is replaced by the puk-puk call at an early age, and the wail seems to be an extension of the whee-u. By 10–12 weeks of age, weep and puk calls are no longer heard and cluck-like sounds begin from females, and growls from males. In general, identifiable calls of younger chicks are limited and might be classified into those maintaining contact with mothers and siblings and (or) expressing contentment, and those expressing anxiety ("where are you" or "I'm lost" calls). By the time chicks are about three-quarters grown, they begin to take on the vocalizations of adults, calls that may be associated with alarm and aggression.[41]

(h) *Brood mixing (shuffling)*. A number of authors have reported brood mixing (e.g., Bendell 1954; Caswell 1954*b*; Weber 1975; Hoffman 1981). This may involve two hens with broods at a particular site (Wing et al. 1944; Fowle 1960; Mussehl 1960; Bendell and Elliott 1967) or one hen with chicks that are clearly of different ages (Wing et al. 1944; Elliott 1965; Weber 1975). The latter might result from (1) after mixing of broods, some chicks may move off with the wrong hen, (2) chicks may stray from their mother, become lost, and join a different brood, (3) after disturbance, chicks that scattered widely may be lost and join a different brood,[42] or (4) a hen may die and her chicks be adopted by another brood female.

How often do "adoptions" occur? We examined records from Comox Burn for all marked juveniles with marked hens that were captured two or more times (n = 115 individuals). Among 137 recaptures,[43] only 5 times was a chick with a different hen in its second or later capture (3.6% of all recaptures). All such birds ranged from ~33 to 69 days of age. Thus, none <33 days of age is known to have switched broods.[44] It is highly probable that contact calls of hens and chicks are sufficiently distinct to provide individual recognition, for even when young broods are mixed by disturbance or use of a common area, chicks most often reassemble with their own mothers. When those of different ages are mixed, hens may be able to identify their own young by their calls because both pitch and volume change with age (J Kristensen, pers. comm.).

Although brood shuffling occurs, hens with broods are most often found alone (Bendell and Elliott 1967), with chicks of the same age and size. Those with young chicks tend to be widely dispersed over the breeding range (Zwickel 1973), which tends to mitigate against mixing.

Another possible explanation for mixing is that broods, or unattached chicks or hens, may join together as flocks. Such groups have been reported while still on breeding range in late summer (Wing et al. 1944; Bendell 1955*a*; pers. observ.). Wing et al. found groups of juveniles of two different ages without hens, and Bendell found two or three hens associated with 10–20 young. Juveniles without females may reflect the

Table 15.4. Summary of calls of females and chicks with suggested functions, based on contexts in which they occur. Asterisks denote calls for which spectrograms are available. F, known from the field; A, known from the aviary.

	Apparent function
FEMALES	
Whinny,* FA	Aggressive, reproductive
Cackle,* FA	Aggressive, reproductive?, spacing?
Liquid cluck,* FA	Aggressive at nest, apprehension?, alarm?
Hard cluck,* FA	Apprehension, alarm, aggressive
Hiss,* FA	Strongly aggressive, nest and brood hens
Post-hatch cluck,* F	Hen on nest "talks" to chicks after disturbance; calming?
Purr,* F	Call to maintain contact with chicks, contentment?
Warble,* F	Alarm, occasionally precedes solid cluck
Solid cluck,* FA	Apprehension, expression of alarm to chicks
Tau-tau,* F	Call to reassemble chicks
Whinny-like call,* F	Sometimes accompanies tau-tau call
Scree, F	Alarm, apprehension by brood hen
Kweer-kweer, F	Alarm, apprehension by brood hen
Kwa-kwa, F	Extreme alarm, apprehension by brood hen
CHICKS	
Weep (peep),* FA	Maintains contact with broodmates and hen, contentment
Puk-puk,* A[a]	Outgrowth of weep, develops at ~2–3 weeks of age?
Purr,* A	Contentment
Whee-u, FA	"Where are you?" call to hen and other chicks
Wail,* FA	"I am lost" call to hen; extension of whee-u
Chirp, F	Curiosity?

[a] Sonogram of the puk-puk resembles that of the chick purr except it has at least two more harmonics.

first stages of brood breakup (see (i) below), and groups of hens with chicks may reflect pre-migratory flocking.

In 1950, but not in 1951 and 1952, Bendell (1955*a*) noted a breakdown, or shuffling, of broods at Lower Quinsam, beginning in mid July. He thought wet weather in July and subsequent lush vegetation might have concentrated broods in [prime] foraging areas in 1950, with brood mixing a result. He proposed that drier midsummer weather in 1951 and 1952 caused a rapid desiccation of the vegetation and may have minimized the tendency for broods to congregate in these areas. We suspect brood mixing in 1950 was a different phenomenon than normal brood breakup and the initiation of natal dispersal.

(i) *Brood breakup.* As chicks grow, they become more and more independent of the hen and by late summer may desert her, or she them. Coincident with increasing independence is a waning of maternal behaviour, as first evidenced by decreasing distraction display. Complete separation from mothers is the first step in natal dispersal, commonly referred to as brood breakup.

Brood organization appears to break down to some extent in mid to late July (Wing et al. 1944) and August (Bauer 1962; pers. observ.) in northcentral Washington, in August and September in the Bridger Mts., MT (Mussehl 1960), and by September in other parts of Montana (Wright and Hiatt 1942). Wing et al. found small "bands" [groups] of juveniles without females in late July and August and suggested (p. 431) that the brood instinct is "rather low" in female blue grouse. They also saw small groups of 2–3 hens without young, but weren't able to tell whether they were brood hens separated from their chicks, non-breeders, or failed breeders. Not all brood hens, however, were separated from their chicks by this time.

Boag (1964) suggested that chicks depart from breeding range with their mothers in the Sheep River area but that they appear to disband enroute to winter range (Boag 1958), as suggested for some birds in northcentral Washington (Wing et al. 1944). Boag first found solitary chicks or small groups of juveniles without hens in September, at elevations above the principal breeding areas. Breeding at Sheep River is quite late, which may explain the late breakup relative to other interior populations.

At Middle Quinsam (Bendell and Elliott 1967) and Comox Burn (Lance 1970), most broods appear to be intact at end of August. What appear to be hens with their own chicks are occasionally found on breeding range into October. They began to disband at Hardwicke Island in late August, and breakup was virtually complete by end of September (Hines 1986*b*).

15.4 Winter

There are few data on winter behaviour of blue grouse because of their mostly arboreal and relatively sedentary lifestyles at this season, coupled with the difficulty of observ-

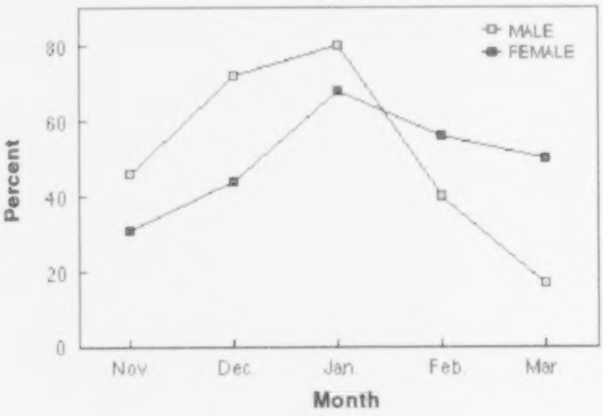


Fig. 15.35. Percentage of grouse in flocks at Hardwicke Island, late autumn to early spring. Data extrapolated from Fig. 2 of Hines (1986*a*).

Table 15.5. Size of winter flocks of blue grouse reported for Middle Park and Hardwicke Island.

Area	No. of flocks	Median or mean	Range	Source
MIDDLE PARK[a]				Cade 1985
Green Mt.	41	3[b]	2–20	
Whiteley Peak	39	4[b]	2–14	
HARDWICKE ISLAND[c]		2.9[d,e]	2–15	Hines 1986*b*
December		~3.6[d]		
January		~3.3[d]		
February		~2.3[d]		

[a] Data extrapolated from Table 6 in Cade.

[b] Median.

[c] Data extrapolated from Fig. 2 in Hines.

[d] Mean.

[e] 1 October to beginning of spring migration.

er access to winter range. Most early work was based on fragmentary observations in which sexes and ages of birds were not identified. With the advent of radio-telemetry, recent winter studies (at Middle Park, Cade 1985; at Hardwicke Island, Hines 1986*b*; at Bear River Range, Pekins 1988; at Miller Ridge, Pelren 1997) allow a closer examination of some activities of the different sex and age classes.

15.4.1 Sociality

(a) *Flocking*. Blue grouse are more social in winter than on breeding range—flocks[45] are common (Caswell 1954*b*; King 1971; Cade 1985; Hines 1986*b*; Pelren 1997). Among 155 winter sightings at Middle Park, 46% involved lone birds, and 54%, flocks (Cade 1985), with no difference between two separate areas [13]. At Hardwicke Island, the percentage of birds in flocks changed from late autumn to late winter (Fig. 15.35), being relatively low in November, increasing in December, and peaking in January. The percentage of birds in groups declined in February and March, more so in males than females. Hines (1986*b*) suggested the greater decline in males than females in late winter may result from social intolerance as males begin returning to, or establishing, territories. Including all birds between 1 October and the beginning of spring migration ($n = 1029$), 52% were found in flocks.

(b) *Size of flocks*. A number of authors have provided snippets of information on the sizes of winter flocks. Caswell (1954*b*) frequently saw those of 6–10 at Brownlee; in some cases loosely associated groups of >20. King (1971) found 12–15 birds together in the Cascade Range of south central British Columbia and flocks of 2–3 males in early winter in subalpine Vancouver Island. After mid January all birds found on his Vancouver Island study area were lone males, presumably adults (four collected were all adults). He was unable to find females and juveniles after they passed through his study area in autumn. At Miller Ridge, 57% of all radio-equipped birds found in trees, December through March, were with other grouse (Pelren 1997). "Mean group size was 3 in December and 2 from January through March" (p. 33), with a maximum of 30. Pekins (1988) examined group sizes by counting tracks on the snow. Among 129 sets of tracks, 34% were made by single birds and 66% were in 30 groups, with a mean of 3, a maximum of 10.

Cade (1985) and Hines (1986*b*) provided the most comprehensive information on size of winter flocks (Table 15.5). Size at Hardwicke Island followed the same general pattern from autumn to spring as for percentage of birds in flocks (Fig. 15.35), peaking in December and January. Winter flocks are small in blue grouse when compared to most North American tetraonines, e.g., white-tailed ptarmigan, 2–80 (Braun et al. 1993); rock ptarmigan, up to several hundreds (Holder and Montgomerie 1993); sage-grouse, up to several hundreds (Schroeder et al. 1999); greater prairie-chicken, up to 300 (Schroeder and Robb 1993); sharp-tailed grouse, up to 30 common, mean of 5–22 in Idaho (Connelly et al. 1998); lesser prairie-chicken (*Tympanuchus pallidicinctus*), may exceed 80 (Giesen 1998); willow ptarmigan, 20–200 common, 1200–2200 reported (Hannon et al. 1998). Winter flocks of spruce grouse (mean of 3, most 2–4, in Alaska (Ellison 1973)) and ruffed grouse (mean of 4 or 5 (Stauffer 1989)) are relatively small, suggesting this may be a characteristic of birds wintering in forested areas. As well, up to 50% or more of wintering blue grouse appear to spend much of their time alone (see above), but this might be low because of the difficulty of finding birds in conifer trees.[46] Nevertheless, results of Cade (1985) and Hines (1986*b*) are generally consistent with other more fragmentary data and strongly suggest blue grouse are often found alone or in small groups in winter. Also, some apparent flocks may represent ephemeral concentrations at feeding sites rather than social groupings. Little is known about the cohesion of flocks of blue grouse, and birds may move in and out them.

(c) *Sex and age composition of flocks*. Juveniles are sufficiently grown by November that they are difficult to separate from adults except in the hand. Thus, Cade (1985) identified birds only to sex. Among 72 lone birds at Middle Park, 17 were males, 35 were females, and 20 were unclassified. Among 83 flocks, 1 had only males; 18, only females; 33, males and females; 2, males and unidentified birds; 26, females and unidentified birds; and 3, only unidentified birds. Although there were more females than males in flocks, the sex ratio did not differ from 1:1. We think the lower number of males than females in flocks and among lone birds indicates some adult males may have been missed, perhaps wintering elsewhere as single birds and more difficult to find. Many, if not most, males found with females may have been birds of the year.

At Hardwicke Island the percentage of birds with others differed among sex and age classes. From 1 October to 31 March, 46% of 127 adult males, 38% of 112 adult females, 57% of 170 juvenile males, and 55% of 267 juvenile females were found in flocks (Hines 1986*b*): ". . . adult females were less apt to be grouped than were juvenile males or females" (p. 422). Grouse were most often associated with others of their own sex and age class; less often, however, in adult females than in adult males and juveniles.

15.4.2 Winter activity

Owing to their migratory habits and heavy use of conifer needles as winter food, most blue grouse, once the ground is snow covered, spend most of their time in conifer trees. Certain trees, or clumps of trees, are clearly selected for, e.g.,

> "If not disturbed too much they will remain in the same clump of trees all winter, not coming to the ground for days at a time . . . The ground under one of these roosting trees, in the spring, resembles a poultry yard with its accumulation of droppings" (Munro 1919, quoted in Wing 1947, p. 505, original not seen by us).
>
> "Under such conifers, droppings may accumulate until a bushel or more lie in one place, especially under isolated and dwarfed trees near timber line" (Beer 1943, p. 34).
>
> "After snow covered the ground in mid-November, the birds spent most of their time in trees, and one might snowshoe an entire day without seeing a track." (Marshall 1946, p. 44).

We know from recent telemetry studies that winter home ranges are larger than these quotes imply (see 17.3.3), but certain trees, or clumps of trees, do receive selective use—perhaps by different birds. King (1971, p. 34) found that ". . . some grouse spent long periods (to at least 8 weeks) in one tree or a clump of trees, others evidently moved about a large area as old sign . . . was occasionally found where grouse were not" (see also 13.5).

Caswell (1954*b*) provided some early behavioural notes on blue grouse in winter. On his area, birds roosting for the night in dense Douglas-firs flew 30–60 m to nearby Douglas-firs or ponderosa pines for morning feeding, commencing about 1/2 h before sunrise. Feeding ceased ~1 h after the first movements. They might then fly to nearby firs or pines or fly to the snow and walk to where they would fly into another tree. Here they rested till midday (1100–1400 h). They sometimes then flew 60–250 m to another tree for no apparent reason. Beginning at ~1600 h they tended to fly to feeding trees in the vicinity of where they would spend the night, roosting in or near these trees.

Although this grouse spends most of the winter in trees, they do come to the ground (Wing 1947; Caswell 1954*b*; King 1971; Pekins 1988; Pelren 1997). On Vancouver Island, King found most birds feeding or loafing in trees but noted that they walk on and roost in the snow—principally in powder snow and away from trees. He and Caswell (1954*b*) thought they entered snow roosts from flight. King reported most such roosts had 18–24 droppings, ~1 night's accumulation, but >100 in some cases [perhaps more than 1 night]. In the Bear River Range, UT, Pekins (1988) found 53 snow roosts, principally in clearings, as reported by King (1971), but none indicated birds flew in. Pekins (p. 98) considered snow roosting "not a predominant" roosting behaviour and thought it peaked during, and 1–2 days after, major snowstorms. He proposed that this behaviour is used for protection from extreme wind and snow conditions.

Among 129 sets of tracks found on the snow by Pekins, 11 were >100 m in length, the longest ~1000 m. Those <100 m in length (>90%) averaged 45 m. Among all sets, 71% were uphill, 28% across hillsides, and 1% downhill. He suggested walking uphill is more energy efficient than flying, and downhill flight, because it is largely passive, is most efficient for downward movement. He seldom saw birds on the snow so thought walking occurred in early morning, that it might substitute for thermoregulatory requirements, and that it might be an important aspect of wintering strategy.

At Miller Ridge, Pelren (1997) found grouse on the ground 169 times between December and the end of March, 32% of all winter locations. Percentage on the ground varied by month: 8% in December, 13% in January, 27% in February, and 57% in March; and ". . . birds on the ground were primarily in areas without snow . . ." (p. 30). He found no snow roosts. If records for March are deleted,[47] the percentage of birds found on the ground would be more in line with indications from midwinter at other areas.

Blue grouse are rarely seen on the ground in lowland coastal areas in winter, where snow seldom accumulates or stays on the ground for extended periods, even though some birds winter there. This likely reflects their near-obligate winter conifer diet, coupled with a mild climate conducive to roosting in trees (see also 13.5).

15.5 Synthesis

Behaviour is of profound importance to all aspects of the life of grouse. Some behaviours are general and similar among different sex and age classes. Others are specific to sex, age, or time of year and include virtually all vocalizations.

Yearling and adult males have at least three clearly defined vocalizations, with songs of coastal and interior males clearly differing in numbers of syllables, frequencies, and audibility. Whooting is a courtship call, and the growl is agonistic and (or) indicative of apprehension. The song and whoot are very low frequency vocalizations.

On breeding range, males are strongly antisocial, and the vast majority are alone when found. Yearlings seldom hold territories, while most adults do. Yearlings tend to be secretive and associate with a small number of adult territories, likely establishing familiarity with an area (and its inhabitants). Adult males spend virtually the entire breeding season on territories they defend from other males. Here they sing, feed, court females, rest, and roost. Courtship involves spectacular display. As polygynists, the range of behaviours of adult males is limited and stereotyped, and most leave their territories once the courtship and copulation season is over. In short, the life of adults males on summer range is principally oriented toward feeding and breeding, that of yearlings toward finding a piece of ground on which they may obtain a territory in subsequent years.

In contrast to males, many yearling, and virtually all adult, females breed and their behaviours are generally similar. Their activities are strongly keyed to different phases of the reproductive cycle, e.g., breeding, nesting, and raising young. They have a much wider behavioural and vocal repertoire than males. The vocal repertoire of females includes at least 20 distinctive calls. Vocalizations are associated with alarm, aggression, nesting, communicating with young, and perhaps with spacing. Frequencies tend to be much higher than in calls of males.

Prior to nesting, hens tend to be alone and secretive. If in breeding condition, they use two calls that appear to be associated with breeding and (or) maintenance of individual space. Some incubating females defend their nests, displaying strong agonistic behaviour.

Once chicks hatch, the hen and her brood move as a unit. Some females defend their broods vigorously with attacks on an intruder, most with at least some level of distraction display, at least when with very small chicks. Cohesiveness of the hen and brood are maintained by vocalizations of hens and chicks.

In the first week after hatch, chicks spend considerable time brooding, amount depending on weather. Non-brooding time is mostly devoted to feeding. Beyond the age of brooding, the young spend much time feeding. Overall, females tend to be antisocial on breeding range, with broodless hens mostly alone and brood hens with chicks, mostly separate from other birds. In mid to late summer they may congregate in small groups, perhaps in response to concentrated food supplies, perhaps in response to a waning of social constraints and preparation for return to winter range.

Winter behaviour is less well known. Nevertheless, birds tend to be more social than on breeding range. Winter flocks are common, though usually small. Flocks often contain birds of both sexes, and males may be juveniles from the previous breeding season. Some data indicate adult males are less social and are found mostly alone. This grouse is largely arboreal in winter, consistent with its food habits, and is seldom found on the snow, or ground, even in snow-free areas.

Endnotes [Chapter 15]

1. For example, does feeding behaviour fit best in a chapter on foods, or in behaviour? – in this case we chose the former. We have cross-referenced such instances when relevant.

2. Except, in some cases, very small chicks.

3. Postures may vary by activity when disturbed, distance at which the bird was disturbed, type of disturbance, and nature of the individual (e.g., wild or tame, dominant or subordinate).

4. Helmcken Island is ~1.5 km^2 and likely has no self-sustaining population.

5. Size may vary with sex and age of the bird and nature of the substrate.

6. Aviary chicks may go through a full sequence of dusting behaviour at ~1 day old.

7. Among 19 other sightings, observers failed to record distances between individuals. If all were within 10 m of other birds, 82% of 207 would be classified as alone.

8. Reported movements within home ranges fall into two classes: those in which sequential sightings of individuals span >1 day and those identified on a daily basis. The first are most often dependent on identifying individuals by reading band combinations, in which case the period between sightings may span days or even weeks. Most day-to-day movements are from radio-marked birds.

9. Some yearlings take territories after removal of established adults (Bendell and Elliott 1967; Bendell et al. 1972; Zwickel 1972*a*).

10. D Maskell (field notes) watched, and heard, a banded yearling male whoot and drop its wings while courting a female at Hardwicke Island. Other sightings of this bird indicate he was territorial that year.

11. Many flushed before detection likely do so from a crouch.

12. Hjorth suggests the tail may be partly fanned, but this may have resulted from his presence. Our description is from McNicholl whose observations were of supposedly undisturbed males.

13. Unless quite close to a bird, one may hear no flight sounds other than at landing.

14. We have no certain records of yearling males landing on loud wing; in one sample of adult male landings, 23% (18/77) were on loud wing, and among eight yearling males, none, a significant difference between age classes.

15. Flutter flights occur within seconds of an appropriate stimulus.

16. Total time recording cantos, 288 min, whoots, 1656 min; flutter flights, 1368 min; all counts combined.

17. Many more males were heard in the background, providing a constant hum on some evenings, but many individuals could not be isolated. The maximum number of singing males that was isolated at a listening station was seven.

18. We suspect most copulations occur in twilight hours, which would explain in part the paucity of observations of this behaviour.

19. Clasping of the female with the wings seems important in maintaining position.

20. Boag (1966) found mixed sex flocks of 2–11 non-breeding "sub adults" [yearlings] on summer range at Sheep River. This has not been reported elsewhere and may relate to the immaturity of birds because of late hatches and early onset of winter in this area.

21. The "whinny" given by brood hens may be a variant of the original described by Stirling and Bendell, or perhaps a different call (Zwickel 1992).

22. The best estimate of the incubation period of blue grouse is 26 ± 1 day (McKinnon and Zwickel 1988).

23. Kristensen watched hens from a blind set up at least 8 h before observations began. He considered his observations to not disturb hens he watched.

24. A dog may even put its nose on the hen before she flushes (Caswell 1954*b*).

25. Observers were asked to record behaviours, but the degree to which they did so varied from none to great detail.

26. If a hen was on a recess, reactions were those expressed on her return to the nest.

27. Clucking has been reported in hens in different situations, including pre-breeding hens, nest hens, brood hens, and during flight from disturbance. There may be subtle differences in this call that have not been discerned by ear — we suspect several calls are included in the generic term "cluck" — more work is needed on vocalizations of females.

28. Data from Comox Burn, Duck Creek, the May Ranch, Skalkaho, and Hudson Bay Mt. combined.

29. Precise data are not available because we tried to minimize disturbance at this time.

30. Distances are those travelled by hens, brood site to brood site. Chicks cover much more ground as they range out from hens and often travel to and from them more than once.

31. This cluck-like sound appears to be a general warning also used by hens at other times than when with brood.

32. Distances vary among populations, tending to be greater than this in those that are more wary than on Vancouver and Hardwicke islands.

33. Uncommon and seems to indicate a very excited hen.

34. A very excited hen may alternately raise and lower her crest.

35. Tail may be vertical and >75% spread or raised >45° and <75% spread.

36. Primaries are spread, and an audible rustle from dragging on the ground may be heard.

37. Observers may sometimes be struck by the wings.

38. Sometimes termed "leading".

39. Kristensen rated the "overall vigor" of distraction display (our "total response") on the basis of which display components were exhibited, the frequency with which they occurred, and how long the display lasted. Overall vigor was rated on a scale of 0–3.

40. Sounds reported only from aviary females include: hoot, whoot, puk (Stirling 1965), croak (Stirling 1965; Cooper 1977), and sneeze, weep, and gluck (Cooper 1977). As with males, we leave analyses of these calls to a more comprehensive future analysis of all aviary behaviour.

41. Other sounds reported only from aviary chicks include cluck (perhaps the chirp noted above) and rattle (Cooper 1977). As with males and females, we leave analyses of these calls to a future more comprehensive analysis of all aviary behaviour.

42. After disturbance and wailing by chicks of one brood, two or more females in the near vicinity may respond by clucking, perhaps attracting chicks not their own.

43. Ninety-four were recaptured once, 20 two times, and 1 three times.

44. We cannot rule out the possibility that some younger chicks switched broods and died but think it unlikely to be many. In late summer some chicks separate from their mothers and join other broods or other chicks without hens. This appears to be the first stage of brood breakup and might explain reports of switching by some older chicks.

45. Workers often have not defined what constitutes a flock, and we presume it is usually defined as ≥2 birds considered as together.

46. Data on sizes (and frequencies) of winter flocks of blue grouse must be viewed with caution because of the difficulty noted. Cade (1985) and Hines (1986*b*) located many birds by radiotelemetry but could have missed non-radioed birds in taller trees. In fact, Hines omitted all birds found in taller trees in his analyses of groupings, introducing possible biases into his data.

47. March is a transition period, with birds starting to move onto, or toward, summer range and should not be considered as winter for purposes here. Snow-free areas are appearing by this time in many areas and years.

CHAPTER 16

Use of Habitat

> *. . . individuals having an innate tendency to choose a favourable environment*
> *. . . and to avoid unfavourable places, are most likely to survive and produce offspring.*
>
> Olavi Hilden (1965)

Birds, and other vertebrates, use their environments selectively (Lack 1933; Miller 1942; Svardson 1949; Jenkins 1953; Wecker 1964; and Hilden 1965, among many others), so-called "habitat selection". This reflects a preferential use of certain parts of the environment and has implications at the evolutionary (Thorpe 1945), species (Cody 1981), population (Bendell and Elliott 1966), and individual (Hilden 1965) levels, and for conservation and management.

Habitat use is a matter of both choice and scale, with choices constrained by attributes of the environment and by physical and behavioural attributes of the species and individual, at times by social phenomena. It may occur at the levels of the landscape (e.g., mountain versus plain and major plant formations—so-called "biomes") and local plant communities, down to a selection of nest sites, songposts, microhabitats for roosting, feeding, etc., or particular parts of a plant as food or cover. It may vary by sex, age, and reproductive status of the individual, and by time.

Features selected usually are not mutually exclusive, making it difficult to interpret their significances, e.g., the line between selection of cover and food is not always clear. A further confounding factor is that while selection can reflect adaptation and "need", it may reflect no more than preference. We review some of what has been reported about habitat use in blue grouse, some anecdotal, most descriptive, and some experimental, adding new observations from our own studies.

16.1 The landscape level

Blue grouse are found mainly in association with coniferous forest, and this might be an aspect for which they select, at least in winter. Although many breed outside forest, as short-distance migrants, they are seldom far from conifers. Others breed within or at the edge of forest, ranging from savannah-like stands of pine, to old-growth coast forest, and subalpine parkland. Clearly, conifers contribute to their "settling response" (Hilden 1965). Since these birds are obligate, or near-obligate, needle eaters in winter, conifers can likely be considered an ultimate factor (in the sense of Hilden) with respect to habitat selection. Conifers seem to be needed within the annual range of mobility of the individual.

Many central and southern interior populations breed in shrub-steppe habitats with few, or no, conifers (see 7.4.2). East of the continental divide they breed in shrub-steppe foothills below lower treeline, but do not move onto the prairies. Proximity of montane conifer forest (for winter) to acceptable breeding habitat may account for their eastern limits. Nevertheless, their southern distribution ends long before that of conifer forest as one moves south beyond the limits of shrub-steppe (high desert) environments and into low desert. Here they may be limited by climatic factors directly, or indirectly, by their effects on vegetation.

In the northern Rocky Mountains, conifer forest used as breeding habitat is more or less continuous with lowland boreal forest, the taiga, which extends both north and east beyond the mountains. However, blue grouse are not known to extend into the taiga. Lodgepole pine, a widely used winter food in montane areas, is replaced by its close relative, jack pine (*Pinus banksiana*), in the taiga, so a lack of winter food does not seem to explain the absence of this grouse from boreal forest. The spruce grouse, another obligate needle eater, is sympatric with blue grouse in many montane areas and does inhabit the taiga, clear across the continent. At the landscape and (or) biome levels, blue grouse must be selecting for more than just conifer forest.

In northern regions, the eastern limits of blue grouse distribution are associated with eastern limits of the major mountain ranges. Montane habitats are heterogeneous mosaics of different plant communities that vary with slope, aspect, altitude, and soils. Boreal forest tends to be more or less continuous, with little relief and is broken only by muskeg, lakes and ponds, riparian systems, and fire-induced seres. At the landscape–biome levels, blue grouse seem to select montane habitats that provide relatively open breeding sites within or near conifers that are accessible for use in winter. Even within their montane range, lowland stands of closed canopy forest north of about 55°N are seldom occupied. Blue grouse breed mainly in the alpine–subalpine ecotone in northern latitudes, suggesting an avoidance of closed canopy forest.

16.2 Plant community and association levels

Most populations of blue grouse are migratory, and it is clear that they are using plant communities and microhabitats for breeding that differ from those used in winter. A seasonal shift toward more open areas for breeding than for wintering may reflect their evolutionary history, their possible derivation from a prairie grouse ancestor (see 5.2.3 and 14.3).

16.2.1 Breeding range

(a) *Coastal old-growth forest and coast forest seres.* Habitat selection by grouse occupying coastal old-growth forest and variously aged seral stages within single plant communities or associations (e.g., in coastal British Columbia) can be subtle and less easily demonstrated than in populations occupying a mosaic of communities. A number of authors have commented on selective use of mature stands of trees and coast forest seres.

In southeastern Alaska, Doerr et al. (1984) found territories of males (*D.o. sitkensis*) 45 times more dense in old-growth forest than in clear-cuts. On Mitkof Island, AK, Brown (1966) found males and females only in mature stands of timber in summer—none was seen on clear-cut sites.

In California, Bland (1993) compared numbers of "hooting groups" (*D.o. sierrae*) inside national parks and wilderness areas in the Sierra Nevada to those in adjacent managed (logged and grazed) forests. Highest densities were in the unmanaged areas, and he concluded (p. 5) that habitats used by territorial males can be described as ". . . open, mature, Abies/Pinus forests". He considered "massive" old-growth trees as important components of male territories for both *D.o. sierrae* (pers. comm.) and *D.o. howardi* (Bland 2002). Further work is needed with these subspecies, for our limited observations of *D.o. sierrae* in California, Oregon, and Washington are in agreement with the suggestion that it is seldom found outside older aged forest.

In contrast, on Hardwicke Island, Niederleitner (1987) found few grouse in mature or advanced second growth when compared to nearby early seral stages after clear-cut logging, in agreement with other observations about coastal populations in this region (Bendell and Elliott 1967; Zwickel and Bendell 1972*a*). Data presented to support these contrasting reports seem convincing, and why grouse in southeastern Alaska (*D.o. sitkensis*) and the Sierra Nevada (*D.o. sierrae*) differ from many *D.o. fuliginousus* populations is not known. Further work is needed on this question.

In an experimental study of habitat selection at Middle Quinsam, Bendell and Elliott (1966) removed territorial males from adjacent *open* and *dense* conifer plantations. Recruiting yearling and adult males selected *very open* and *open* habitats, and avoided *dense* and *very dense* habitats. Established birds, however, remained on site in dense habitats as conifers grew up around them. A principal implication is that after the forest canopy reaches a certain threshold, recruitment ends and a population will decline as a function of the death rate of adults. This experiment indicated that recruitment ended when tree canopy cover averaged ~75%. Among 49 sightings of females, 88% were in *open* or *very open* habitats.

Other data also imply a selective use of locally distinct plant associations. At Lower Quinsam, Bendell (1954) found a strong preference for "Clover Open" by hens with chicks. This was one of five "open" shelter types he described, and the others received much less use. Two "dense" shelter types were little used. Hens with broods at Lower and Middle Quinsam were often found in ". . . pockets or depressions with lush vegetation" (Bendell and Elliott 1967, p. 51), or were associated with moist areas (Elliott 1965). Observations at Comox Burn and Hardwicke Island agree with these reports, although these data have not been quantified. Two yearling hens that nested in dense forest at Comox Burn moved more than 1 km with their broods to young, open seres immediately after hatch (Sopuck and Zwickel 1992). Females that lost nests or broods while occupying open, young seres moved into dense forest almost immediately (10/30), or used more dense cover within open areas than those with broods. At Middle Quinsam, hens with young broods preferred habitats with little canopy cover but used areas with greater cover as chicks matured, likely reflecting changing requirements of chicks (Armleder 1980). In general, *very open* and *open* habitats were selected, *dense* habitats used as available, and *very dense* habitats avoided.

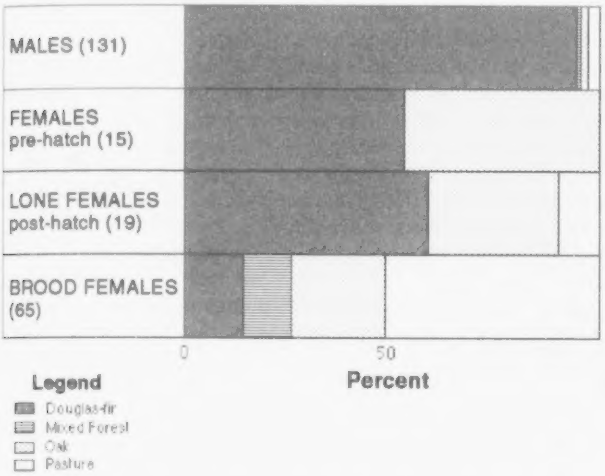
(b) *Coastal community mosaics.* We know of only two intensive studies of coastal blue grouse that occupied a mosaic of clearly different plant communities in breeding season, that of Donaldson and Bergerud (1974) on Prevost Island and our study at the May Ranch.

Males and females on Prevost Island used different community types selectively (Donaldson and Bergerud 1974). Numbers of singing males were greater in the *Douglas-fir Logging Mosaic* than expected on the basis of availability. Numbers were lower than expected in even-aged Douglas-fir with closed canopies and in communities with little or no Douglas-fir. Brood females used small pastures (mean size = 0.8 ha) surrounded by forest more often than expected, but none was found in two large pastures. They used the *Douglas-fir Logging Mosaic* more often than expected but avoided closed canopy forest and three open, xeric communities. Donaldson and Bergerud concluded that males preferred forest of irregular heights, with a patchy shrub layer and a discontinuous canopy. Highest densities were in areas with ~50% tree canopy, lowest densities in areas with closed canopies. Habitats used by broodless females were similar to those in which males were found. An extensive herb layer and proximity to cover were considered important for broods.

Among four major plant communities at the May Ranch (Table 7.2), no grouse were found throughout spring and summer in *Scrub*. Males were virtually confined to the *Douglas-fir* community (Fig. 16.1). Lone females were most often in *Douglas-fir* or *Oak*, and brood females were most often in *Pasture* or *Oak*, the more open communities. Although the entire area, except *Scrub*, can be considered as breeding habitat for this population, grouse differed in their use of communities by sex, and, in the case of females, differed between females with and without brood. As at Prevost Island, brood females were more often in open community types than were males or lone females.

Principal communities where the different classes of birds were found in relation to each other (Fig. 16.1) does not show selection as it relates to the availability of each community. To detect selection in relation to availability, we compared number of sightings of each class of birds within each community to the amount of that community on the study area (Table 16.1). Males used *Douglas-fir* more often than expected, *Mixed Forest* as available, and *Oak* and *Pasture* less than expected [1]. Lone females used *Douglas-fir* and *Mixed Forest*

Fig. 16.1. Sightings of males, lone females (pre-hatch), lone females (post-hatch), and brood females in different plant communities (by %) at the May Ranch, 1985. Sample sizes are in parentheses.



as available or more than expected, *Pasture* less than expected, and selected for *Oak*. In contrast, brood females used *Douglas-fir* less than expected, *Mixed Forest* and *Oak* more than expected, and *Pasture* as available. Brood females avoided *Douglas-fir*, with its dense conifer canopy (Table 7.2), and used more open communities. Avoidance of *Scrub* by all sex and age classes may reflect its xeric conditions, as at Prevost Island.

(c) *Interior community mosaics.* Many interior breeding areas are composed of mosaics of plant communities dominated by very different structural forms, e.g., a mixture of shrub-steppe and trembling aspen or shrub-steppe (or grassland) and conifer forest. The Skalkaho area provides a good example of the latter.

Vegetation there consisted of four principal plant communities, three of which were dominated by ponderosa pine or Douglas-fir (Table 7.2). Martinka (1972) reported that male territories there always included thickets of young conifers associated with openings that were dominated by herbaceous plants. Openings were used for display and considered important because they provided "ready surveillance of the territory" (p. 509). Thickets were considered important as cover.

During our studies at Skalkaho (1986), males were virtually always found in conifer dominated communities (Fig. 16.2), mainly *Douglas-fir*. Lone females followed a similar pattern but tended to use *Ponderosa Pine*, a more open forest type, more than males. In contrast, brood females were most often in areas dominated by open ponderosa pine and tended to use *Bunchgrass* more than males or lone females. As at the May

Table 16.1. Selection, or avoidance, of major plant communities by males, pre-hatch females, post-hatch lone females, and broods at the May Ranch, Duck Creek, Skalkaho, and Hudson Bay Mt.

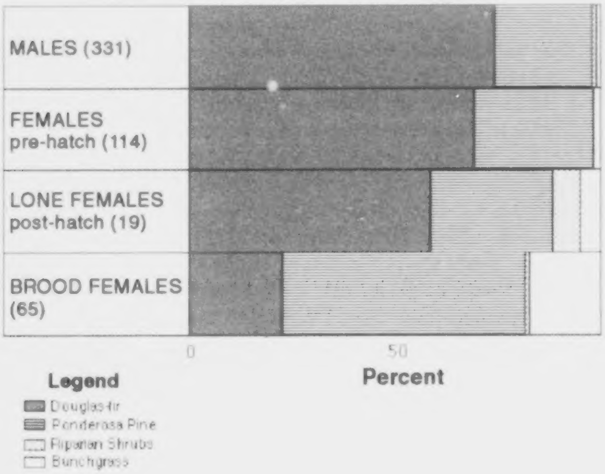
Area, class of birds	Community type			
MAY RANCH	Douglas-fir	Mixed forest	Oak	Pasture
Males	+	o	–	–
Pre-hatch females	o	o	+	–
Post-hatch lone females	+	o	+	–
Females with brood	–	+	+	o
DUCK CREEK	Aspen	Mt. mahogany	Ripar shrub	Sage[a]
Males	+	o	+	o
Pre-hatch females	o	–	+	o
Post-hatch lone females	o	–	+	o
Females with brood	+	o	+	–
SKALKAHO	Douglas-fir[b]	Ponder pine	Ripar shrub	Bunchgrass
Males	+	–	o	–
Pre-hatch females	+	–	o	–
Post-hatch lone females	+	o	+	–
Females with brood	–	+	o	o
HUDSON BAY MT.	Subalpine fir	Kruppelholz	Meadow	Alpine
Males	+	o	o	–
Pre-hatch females	+	o	–	–
Post-hatch lone females	o	o	o	–
Females with brood	–	o	+	–

Note: Symbols: +, habitat used more than as available; –, habitat used less than as available; o, habitat used as available. All categories based on *G* tests; pluses and minuses significant at $p < 0.05$, o's not significant.

[a] Includes *Big Sage* and *Black Sage* communities (Table 7.2).

[b] Includes *Douglas-fir* and *Douglas-fir Thinned* communities (Table 7.2).

Fig. 16.2. Sightings of males, lone females (pre-hatch), lone females (post-hatch), and brood females in different plant communities (by %) at Skalkaho 1986. Douglas-fir includes Douglas-fir Thinned. Sample sizes are in parentheses.



Ranch, broods were most often in communities with the greatest herbaceous cover. Heavier use by broods of *Ponderosa Pine* than the more open grasslands may reflect desiccation of many of the herbaceous species on the more xeric *Bunchgrass* sites.

Males and lone females selected *Douglas-fir*, used *Bunchgrass* less than expected, *Ponderosa Pine* less than expected, and *Riparian Shrubs* as available (Table 16.1) [1]. In contrast, brood females used *Douglas-fir* less than expected, selected for *Ponderosa Pine*, and used *Bunchgrass* and *Riparian Shrub* communities as available. Grouse at Duck Creek (1985) and Hudson Bay Mt. (1986) also exhibited strong selection among different plant communities (Table 16.1) [1].

Use of open habitats by hens with chicks most likely reflects a selection for needs of the young. With very young chicks, it may relate at least in part to an abundance of invertebrate foods (Beer 1943; Wing 1947; Armleder 1980; Sopuck and Zwickel 1992; but see 16.3.3).

16.2.2 Winter range

Blue grouse are largely confined to conifer forest in winter, in stands dominated by a number of different species of trees, alone, or in combination. Occupied habitat can range from coast forest near sea level to subalpine forest, with many birds wintering at high elevations, e.g., on Vancouver Island >1220 m (King 1971), in Idaho >1800 m (Marshall 1946) and >2285 m (Stauffer and Peterson 1985), and in Colorado >2530 m (Cade and Hoffman 1990).

More than 94% of 57 winter observations of blue grouse in southeastern Idaho were on high-elevation (>2440 m) ridges and slopes (Stauffer and Peterson 1985). Birds were found only in the *open conifer type*, a community identified as having <60% tree cover. Frequencies of occurrence of the most common trees at sighting locations were as follows: Douglas-fir, 88%; subalpine fir, 60%; limber pine, 47%; and trembling aspen, 26%. Frequencies of occurrence of the most common shrubs were snowberry, 37%; big sagebrush, 35%; and gooseberry (*Ribes* sp.), 7%; species often associated with open conifer forest. "Areas with 45% to 55% tree cover dominated by 'wolf' Douglas-fir (single or in clumps) constitute the preferred sites used by blue grouse during winter" (Stauffer 1983, p. 88).

Stauffer and Peterson conducted their studies by walking transects and were dependent on seeing or flushing grouse, or finding droppings, to identify areas of use. Since blue grouse are largely arboreal and confined to conifers in winter, this may introduce observational biases among species of trees with different growth forms or in different habitat types. Cade and Hoffman (1990) minimized this problem by equipping grouse with radios. They studied birds on winter range dominated by Douglas-fir in Middle Park. Low densities of small conifers (<70 trees/ha) or high densities of mature trees (>1200 trees/ha) were avoided. They indicated that maturing second growth (50–70 years of age) may represent the earliest stage of development acceptable as winter habitat and found no apparent selection for particular elevations, aspects, or other physical features of the environment. Sixteen birds moved 3–28 km and wintered at higher elevations in lodgepole pine and spruce–fir. It was unclear whether these movements involved habitat selection or were related to social, or other, phenomena.

Many populations are associated with Douglas-fir and (or) true firs, and in general, the distribution of Douglas-fir and some species of true firs is similar to that of this grouse. This led Beer (1943) to suggest that its distribution is limited by the occurrence of these species. However, blue grouse winter in areas in which neither Douglas-fir nor true firs are found, e.g., in very open, savannah-like stands of limber pine in parts of the Great Basin (Zwickel and Bendell 1986), in forests dominated by western hemlock (Hines 1987) and Sitka spruce in coastal British Columbia, and, perhaps, outside conifer forest in northern Colorado (Rogers 1968). Johnsgard (1983) suggested that the general correspondence of much of the range of blue grouse with that of Douglas-fir and true firs is likely because both are adapted to a common climate and community type.

Hines (1987) reported that young grouse on Hardwicke Island preferred mature forest in winter, although some used young seral stages (<20 years of age). Mid-successional forest (51–100 years of age) was avoided. Juveniles wintered at a broad range of elevations, but tended to use those above 300 m. Young males tended to winter at higher elevations than young females, but there was a wide range of overlap (males at 180–670 m, females at 60–580 m). Hines thought use of young seral stages in winter may be more common than reported earlier. Winter use of young stages on Hardwicke Island, however, may be associated with local composition of the forest. Mature and older second growth was dominated by western hemlock and most post-logging seres were replanted with Douglas-fir. Major winter foods were western hemlock, and Douglas-fir, with juveniles eating mainly Douglas-fir (Hines 1987). A preference for this tree, mainly available in plantations, may explain much of their use of these areas.

On nearby Vancouver Island, King (1971) searched lowland areas at Comox Burn and vicinity in winter with a trained dog when he could not find hens and chicks in the subalpine, without success. We found virtually no grouse on our lowland study areas on Vancouver Island prior to 1 April and can document the arrival of significant numbers onto these areas in

April. Also, Sopuck (1979) found that virtually all radio-equipped birds moved off study areas there to higher elevations by early September. Two radio-equipped broods monitored during autumn migration (Lance 1970; Sopuck and Zwickel 1992) were in subalpine parkland when last found, although they may or may not have wintered in these areas. We agree with Hines that some hens and chicks may winter below subalpine parkland, but doubt that they are on lowland clear-cuts in significant numbers. Hardwicke Island, with a maximum elevation of 800 m, no subalpine community, and with Douglas-fir largely restricted to plantations, seems a special case. Nevertheless, on the basis of what appear to be reliable anecdotal reports and a few observations by us, some individuals can be found in winter in mature forest at or near sea level.

The most recent winter study of blue grouse was at Miller Ridge (Pelren 1997). Radio-equipped juveniles and adult males and females selected strongly for "parkland" (<10% tree canopy with <30 m between trees), used "forest" (>10% tree canopy) as available, and avoided "grassland" (>30 m between trees). Juveniles used less densely forested sites and smaller trees than adults, with adults in more clumped stands.

16.3 Selected examples of habitat use

16.3.1 "Cover"

Cover (shelter) may provide preferred microclimates and protection from adverse weather; concealment, or avenues of escape from predators. It also may be used as a source of food. The separation of these functions is sometimes difficult to evaluate, for they may, or may not, be exclusive of each other. Cover may vary among, or on a smaller scale within, communities. Many references to the use of, or need for, protective cover appear to be intuitive or anecdotal. This does not mean they are in error, but they should be viewed with care. There are few quantitative data available from which to draw conclusions about why grouse use particular cover.

(a) *Effects of fertilization on use of cover.* In an experiment at Middle Quinsam, urea fertilizer was applied to a series of 10 plots, in part to see if this would affect the local distribution of grouse on breeding range (Ash 1979). Nitrogen levels, amount of herbaceous cover, plant biomass, and production of flowers and fruits increased greatly on treated plots. Brood females selected fertilized habitat, but "Fertilization did not seem to affect . . . the distribution of territories [of males] or nests" (Ash 1979, p. 94). Irrespective of fertilization, territorial and non-territorial males and lone females used denser habitat (cover) than brood females.

16.3.2 Territorial males

Male territories are usually spaced (Boag 1966; Bendell and Elliott 1967; Martinka 1972; McNicholl 1978) on areas with relatively uniform vegetation structure. Virtually all workers agree that males select open areas within which to display, e.g., open areas for courting (Bendell and Elliott 1967); open stands of trees or shrubs (Rogers 1968); clumps of trees with canopies of ~50%, surrounded by openings (Boag 1966); open Douglas-fir or pine forest associated with young thickets (Martinka 1972); tree or shrub cover with open canopies and understories (Hoffman 1981). In older coast forest on Hardwicke Island, territories were usually near openings (Niederleitner 1987) [but see 16.2.1(a) and Doerr et al. 1984].

Although territories are usually spaced, Lewis (1985*a*) found a tendency (not significant) for them to be clumped near aspen thickets on shrub-steppe habitat at Frazer Creek. He suggested that clustering at and around thickets may indicate a preference for them and relate to patchiness of the habitat.

A strong tendency for males of interior subspecies to sing from the ground and for coastal subspecies to sing from trees (Table 16.2) has long been recognized (Brooks 1926; Bent 1932). Even males of south coastal subspecies (*D.o. sierrae* and *D.o. howardi*) that occupy interior-like habitats, sing mainly from trees (Bland 1993; pers. observ.). Data from two interior × coastal "hybrid" populations that inhabit subalpine areas suggested males there used ground and tree songposts about equally. Many data for the latter populations were collected while the ground was snow covered, and this may have induced more males to sing from trees.

Although coastal males normally sing from trees, they readily adapt to terrestrial songposts on some large coastal clear-cuts (Zwickel 1992), i.e., trees are not necessary. As succession advanced at Comox Burn and Hardwicke Island (Fig. 16.3), males more often used elevated songposts: trees, stumps, and logs (Fig. 16.4) [2a, b]. Increased use of heights as the forest regenerates may aid in the broadcasting of song, the ability to see potential mates, rivals, or predators, and the ability to be seen by potential mates. Any, or all, of these may be involved.

Use of trees in early stages of forest succession is limited by inability of the branches to support this large grouse. Prior to the availability of trees ≥~4–5 m in height, coastal birds on clear-cuts often select small elevations from which to sing and display (Bendell and Elliott 1967; McNicholl 1978), especially during peak breeding. As the peak is passed, they more often sing from within, or at the edge of, small thickets, presumably for reasons of cover. Interior males (that usually sing from the ground), however, often establish territories near aspen thickets, which are usually in gullies or depressions, the

Table 16.2. Percentage of male blue grouse found singing on the ground, logs, stumps, or trees for interior subspecies, south-coast and north-coast subspecies, and "hybrid" populations.

Region (*n*)	Ground	Log	Stump	Tree
Interior[a] (382)	92	5	1	2
South coast[b] (65)	20	0	0	80
North coast[c] (113)	3	0	0	97
Hybrid[d] (79)	42	2	5	51

Note: *n* values are in parentheses.

[a] *D.o. obscurus* from Arizona (3), Colorado (1), and Wyoming (2); *D.o. oreinus* from Nevada (4); and *D.o. pallidus* from Montana (178) and Washington (194).

[b] *D.o. sierrae* from California (22), Oregon (33), and Washington (10).

[c] *D.o. fuliginosus* from California (107) and *sitchensis* from Alaska (6); excludes populations inhabiting clear-cut forests.

[d] *D.o. pallidus* × *D.o. fuliginosus* from northcentral Washington (19) and *D.o. richardsonii* × *D.o. fuliginosus* from westcentral British Columbia (60).

Fig. 16.3. Change in use of songposts of males with advancing succession, Comox Burn (1971–1972, 1976–1977) and Hardwicke Island (1979–1981, 1982–1984). Total *n* values for each period are in horizontal bars.

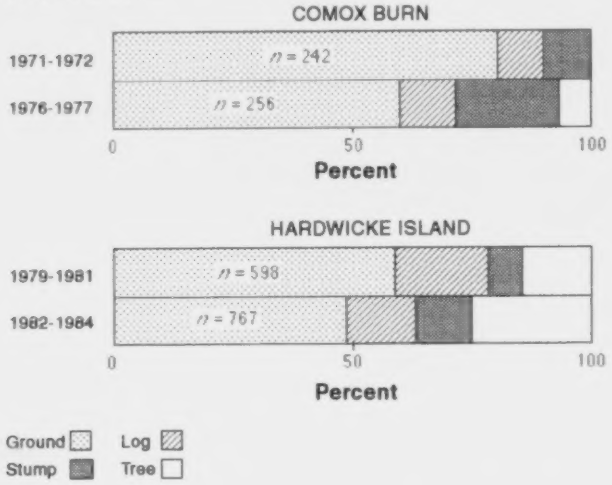
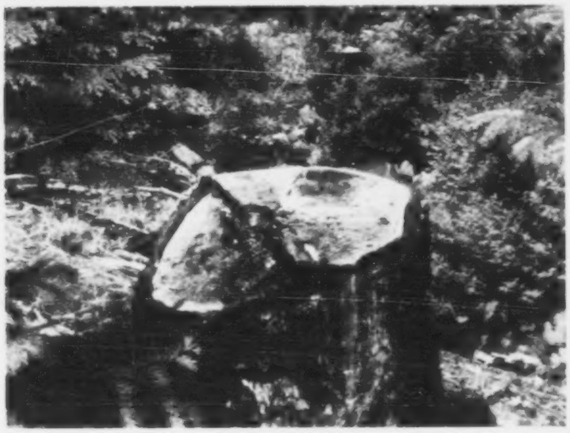


Fig. 16.4. Hooting posts can often be identified by accumulations of rectal droppings, as on this stump, Comox Burn, June 1976.

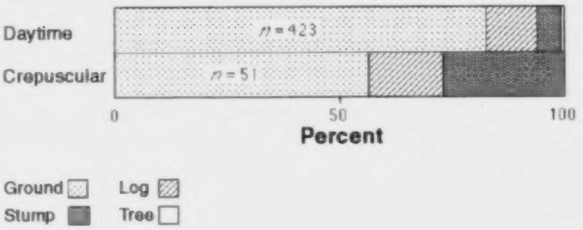


lower sites among those available. This suggests access to cover (thickets) may be more important than height.

A male may sing from more than one location within its territory (Bendell and Elliott 1967), usually 3–4, up to seven (McNicholl 1978), and sites used may vary with time of day. In early morning and evening, coastal males tend to select high points from which to sing more often than during the day, as indicated by a significant increase in use of logs, stumps, and trees at these times (Fig. 16.5) [3]. Although our records lack sufficient detail for analysis, it is our impression that local heights (classified as ground locations) are used more in early morning and evening than during the day, as with logs, stumps, and trees.

Males also select particular species of trees from which to sing. Among 223 arboreal songposts in which the species of singing tree was identified, 222 were in conifers[1] (Table 16.3) even though some deciduous species were available at virtually all areas. At most locations, principal species used were those most abundant, but selection or avoidance would be difficult to document without detailed information on availability of the various species. Nevertheless, what appears to be a clear avoidance of deciduous species and of western red cedar (common at some coastal sites) and white and lodgepole pine (common at some coastal and interior sites) suggests species-specific selection. Trees used for singing also are often used for foraging (Zwickel 1992). Birds may sing from trees selected for foraging, or vice versa, or may involve both. In the Sierra Nevada of California, Bland (1993) considered "massive" trees (>122 cm DBH) used as hooting posts an important component of territories.

Fig. 16.5. Location of songposts of males at Comox Burn during daytime (between 08:00 and 18:00 h) and crepuscular (at or before 08:00 h, at or after 18:00 h) hours, 1971–1973.



16.3.3 Broods

Hens with broods often use open, semi-open, and (or) mesic areas from within those available (Marshall 1946; Bendell and Elliott 1967; Donaldson and Bergerud 1974; Hoffman 1981; Niederleitner 1987; see also 16.2.1). The most common explanation for this is that such areas are important foraging areas for chicks (Beer 1943; Wing 1947; Armleder 1980). These sites also may provide better cover or greater comfort than more xeric plant associations, however, especially on interior breeding ranges. Teasing the relative importance of these functions apart will require careful study.

A healthy herbaceous understory (mainly broad-leaved herbs) and (or) a high degree of interspersion of various plant life forms are regularly cited as important components of brood habitat (Mussehl 1963*a*; Harju 1974; Hoffman 1981; Stauffer 1983; Zwickel and Bendell 1985; Niederleitner 1987). Hoffman suggested that heavy ground cover is avoided and that light to moderate grazing by domestic livestock has little effect on brood habitat, but that if most herbs were removed, broods moved to less disturbed sites. Mussehl, too, considered overgrazing to be detrimental to broods. He emphasized the need for concealment and escape cover for prime brood habitat, but did not consider food or microclimate as possible functions of such cover.

On some areas, hens with chicks are seldom found more than 50 m from taller shrubs or trees (Mussehl 1963*a*; Weber 1975; Hoffman 1981), either of which may be used as escape cover. Healthy populations of blue grouse occupied Comox Burn, however, in the first 3–4 years after wildfire, a period during which shrub and tree cover was extremely sparse (Zwickel and Bendell 1967*b*). Our impression is that birds

Table 16.3. Species of trees[a] in which males were found singing (by %): interior subspecies, south-coast and north-coast subspecies, "hybrid" populations, and at Hardwicke Island.[b]

Region (*n*)	Species of tree				
	PIPO	PSME			
Interior[c] (9)	22	78			
	ABCO	ABMA	PIPO	PSME	
South coast[d] (45)	22	20	44	13	
	PICO	PISI	PSME	QUsp	TSHE
North coast[e] (100)	1	2	95	1	1
	ABLA	PICO	PSME		
Hybrid[f] (35)	54	9	37		
	PISI	PSME	THPL	TSHE	
Hardwicke Island[g] (34)	3	9	9	79	

[a] ABCO, *Abies concolor*; ABMA, *A. magnifica*; ABLA, *A. lasiocarpa*; PICO, *Pinus contorta*; PIPO, *P. ponderosa*; PISI, *Picea sitchensis*; PSME, *Pseudotsuga menziesii*; QUsp, *Quercus* sp.; THPL, *Thuja plicata*; TSHE, *Tsuga heterophylla*.
[b] *n* values are in parentheses.
[c] *D.o. pallidus* from Montana (7) and Washington (2).
[d] *D.o. sierrae* from California (16), Oregon (21), and Washington (8).
[e] *D.o. fuliginosus* from California (96) and *D.o. sitkensis* from Alaska (4); excludes birds in clear-cuts.
[f] *D.o. pallidus* × *D.o. fuliginosus* from northcentral Washington (14) and *D.o. richardsonii* × *D.o. fuliginosus* from westcentral British Columbia (21).
[g] Birds in residual patches of mature forest only; excludes birds in clear-cuts.

there tended to "freeze" until approached very closely rather than to flush or run to physical cover, perhaps a behavioural adaptation to the sparse vegetation. As ground cover increased, they more readily ran or flushed when approached. If true, this reflects a behavioural adaptation to absence or presence of concealing cover.

Habitats used by broods may change as the season advances. In Montana, young broods were most often in grass–forb associations but by late July were often in deciduous thickets (Mussehl 1960), a pattern also documented in shrub-steppe habitat in northcentral Washington (Zwickel 1973). Broods in coastal areas also tend to move from open to more dense plant associations with age (Armleder 1980). Increased use of fruit-bearing thickets as summer advances may relate to the ripening fruits. Use of others, such as a tendency to move into aspen dominated associations within shrub-steppe communities (Zwickel 1973), may reflect a selection for a cooler or more mesic microclimate as vegetation in more open areas desiccates. For example, on the Frazer Creek study area, walk-in traps within aspen thickets caught virtually no birds, while those along the outside edge of, or between, thickets were productive (pers. observ.). Grouse were commonly found in aspen thickets, however, and trapping data suggest they were mostly sedentary while there. In summer, aspen thickets appeared to be used mainly for loafing, a comfort activity.

16.3.4 Winter roost and feeding trees

There is much observational evidence that blue grouse select particular trees for feeding and (or) roosting in winter. For example, Marshall (1946) found droppings up to 2.5 cm deep under certain trees, suggesting their selection. Birds were most often in Douglas-fir trees, although whitebark pine, subalpine fir, and Engelmann spruce were present, again indicating selection [no data on the relative availability of the different species was provided]. Wing et al. (1940) also noted extensive winter sign under Douglas-firs, with less under whitebark pine, and virtually none under spruce. They indicated that dwarf trees near upper treeline were most heavily used in winter.

Other observers (Caswell 1954*b*; Boag 1958; Stauffer 1983; Pekins et al. 1991) have suggested that atypical trees, especially those with dense foliage at upper treeline, are used selectively in winter. Wing (1947) thought stunted trees near timberline were selected and that birds wintering at lower elevations tended to use large trees, mainly Douglas-firs, from among those available. King (1971) reported a selection for large trees in subalpine parkland situations on Vancouver Island and that dense, scrubby trees on exposed ridges were used mainly in calm weather. He worked mainly with adult males, however, and proposed that hens and juveniles might winter in different habitats.

Some workers have provided quantitative information on selection of particular species of trees in winter. In Idaho, 36 of 38 winter roost trees (95%) were Douglas-fir, with one subalpine fir and one Engelmann spruce identified (Stauffer and Peterson 1986). Most roost trees were apparently found by flushing birds during daylight, however, so those used at night may not be represented.

Forests on Cade's (1985) Whitely Peak and Green Mt. study areas were dominated by Douglas-fir and (or) subalpine fir. Eighty-six percent of winter sightings were in Douglas-fir, although its occurrence in a random sample was only 31%. Within stands, larger trees were selected. In a mixed stand of lodgepole pine and Douglas-fir, grouse preferred pine. Cade proposed four possible reasons for this selection: protein maximization, avoidance of secondary compounds, protection from predators, and selection of favourable microclimates. Where Douglas-fir and pines are mixed with lowland firs and (or) subalpine fir and spruce, true firs and spruces appear to be used principally for roosting, with Douglas-fir and pines preferred for foraging (Cade 1985; Zwickel and Bendell 1986; Pekins et al. 1991).

The suggestion that blue grouse select certain trees for feeding and roosting in winter led Pekins et al. (1991) to examine this relationship with radio-marked birds. Ninety percent of diurnal "use-trees" were Douglas-fir, and 70% of nocturnal use-trees were subalpine fir, both greater than expected on the basis of availability. Nocturnal use-trees, mainly subalpine fir, had greater canopy cover than those used during the day, mainly Douglas-fir. Douglas-fir use-trees were significantly shorter, and subalpine fir use-trees, significantly taller, than the average for each species, respectively (Pekins 1988). See also 12.5.1(c).

Pekins (1988) also studied microclimatic characteristics of winter roost sites. He concluded (p. 73), "Douglas-firs provided exposure to solar radiation, wind protection, and a food source during the day. The nocturnal use of subalpine firs increased protection from winds and provided near maximum canopy coverage", and (p. 49), "The use of subalpine fir predominantly at night is likely related to the selection . . . of a better microhabitat since they seldom eat subalpine fir." These results indicate microclimate may be an important component of winter habitat selection. This was a unique study in that it provided virtually the only information available on blue grouse at night and demonstrated relationships that could not have been recorded without radio-telemetry or by diurnal work alone.

Also see 10.5.1 and 12.1.3 and 12.1.4 for information on nest site and food selection.

16.4 Synthesis

Habitat selection represents a matter of choices, but the difference between those that may be adaptive or those that are merely a matter of preference is difficult to determine. If adaptive, and particular habitats are limited, it may have important implications to the species, population, or individual. If mere preference and particular habitats are not limited, it may be less significant.

It seems tautological to point out that blue grouse [and other organisms] use habitats to which they are adapted, but this emphasizes that selection does occur. Much of what we know, or think we know, about habitat use in blue grouse derives from general observations, comparative studies, and anecdotal reports. There are few experimental studies. Some points are clear, others less so.

At the landscape and biome levels, this grouse is confined to north temperate and subarctic cordilleran regions of western North America. Although steppe or shrub-steppe habitats often serve as prime breeding range and the more or less continuous forest of the taiga appears suitable as winter range, this bird does not move far from montane conifer forest into these communities. Virtually all populations studied use open, or relatively open, habitats, or openings within more dense habitats, for breeding, and montane conifer forest as winter range. Use of relatively open breeding areas in near proximity to coniferous winter range may reflect the evolutionary history of blue grouse; e.g., systematically, they appear intermediate between prairie, or shrub-steppe, and forest tetraonines, even though they are usually classified as a forest species.

At the community level, north-coast subspecies occupy old-growth and seral conifer forest communities in breeding season, in very high densities in some young seres following clear-cut logging or fire. Where conifer forest borders deciduous forest or non-forest (plant community mosaics), there may be clear differences in use of the different community types by sex and age classes. Especially notable is that young birds stop recruiting to forest seres with closing canopies, and males and broodless females tend to use more dense vegetative types than nesting females and those with broods.

Interior breeding areas are often composed of mosaics of structurally different plant communities, e.g., shrub-steppe mixed with deciduous and (or) conifer forest. Here, males and broodless females tend to be found in, or near, forest types, while females with broods tend to use shrub-steppe, open forest, or openings within the forest.

In winter, blue grouse are largely confined to conifer forest, but the species composition of occupied communities may vary. Early suggestions that they might be limited by the distribution of Douglas-fir and true firs, or to areas at high elevations, in winter, are now known to be untrue.

There are many cases where birds of given sex and age classes are clearly selecting, or appear to be selecting, particular habitats, or parts of them. We cite only a few examples but emphasize that even where selection occurs, it may reflect either "preference" or "need". The first is of less interest than the latter, which may have important implications to behavioural, population, and evolutionary theory, and to conservation and management.

Endnote [Chapter 16]

1. Includes data for initial locations only. If flushed into a deciduous tree, males may sing from there, at least temporarily.

CHAPTER 17

Movements and Use of Space

Migration, dispersal, site fidelity, and home range are special aspects of behaviour that deserve individual attention. We present this chapter in three sections: (1) Migration, (2) Dispersal and Site Fidelity, and (3) Home Range, all of which relate to movements and use of space.

17.1 Migration

> *Ever since man became capable of reasoning he has speculated about the movements of birds—where do they come from; where are they going; what impels them to take these . . . journeys; . . .*
>
> GC Aymar (1938)

"Migration is specialized behaviour especially evolved for the displacement of the individual in space" (Dingle 1980) and, by this definition, includes dispersal. Dingle used this definition because of the great variation in kinds of movements among different groups of animals. Among ornithologists and some ecologists, however, migration is commonly defined as seasonal to-and-fro moves between breeding and wintering areas (Wallace 1955; Dorst 1962; Welty 1964; Carlquist 1965; Yapp 1970; Smith 1974, among others). This allows an individual to use habitats only seasonally available and (or) to avoid seasonal adversity. Many species show high fidelity to breeding and wintering areas, so once such sites are established by an individual, this migratory pattern persists.

17.1.1 Nature of migration in blue grouse

The first recognition of which we are aware that blue grouse might be migratory was by George Suckley and was based on observations by early settlers that these birds mostly disappear in autumn (Cooper and Suckley 1860; Suckley 1860). Other settlers thought they spent ". . . the [winter] season [in tall fir trees] in an almost immovable state of hibernation" (Baird et al. 1874, p. 425). Although often classified as non-migratory, most populations move locally: from relatively open breeding areas in summer into montane conifer forests in winter, usually at higher elevations (Anthony 1903; Wing 1947). Vertical migrations are common in montane areas but that of most blue grouse is "inverted" (Welty 1964, p. 457), with individuals moving up to winter, down to breed (Swarth 1912; Bent 1932; Gabrielson 1940; Burleigh 1972, among others), the reverse of that recorded for most species[1]. Some individuals move into subalpine areas near upper treeline to breed, and presumably down into more dense conifer forest for winter. And some individuals (Hoffmann 1956; Rogers 1968; Cade 1985; Hines 1986*a*; Pelren 1997) may be non-migratory, breeding and wintering in the same general area.

Breeding is common at or near sea level on the northwest coast, and some birds winter there. Winter sightings at lower elevations are very uncommon, however, and we believe most birds move up in winter. In parts of southeast Alaska, some may move up in early autumn and down to coast forest at or near sea level to winter (Bailey 1927), but this is not documented for known individuals. As noted elsewhere (4.2.6), some small coastal islands with little relief have breeding populations, and whether grouse remain there in winter is not known, but if so, they would be considered non-migratory.

The nature of migration in this bird is thus variable, with some populations and (or) individuals perhaps not migratory. Nevertheless, most appear to move seasonally between breeding and wintering areas. Variations likely relate to the proximity of breeding areas to winter habitat.

17.1.2 Migratory behaviour

(a) *Spring.* Migratory behaviour in spring has not been examined in detail, but a number of authors have recorded observations of birds presumed to be migrating. The first, perhaps the most extensive, description was for birds in northeastern Oregon. There, Anthony (1903, p. 25) described birds moving from forested winter areas at upper elevations to lowland breeding range:

> "From the higher slopes . . ., the birds sailed until the rising ground brought them to the surface of the snow on the south side of the creek, usually well above the canyon. From this time until the highest point of the ridge south was reached the journey was performed on foot."

Anthony says grouse arrived on Baldy, a high conical peak, as singles, pairs, and small flocks, with hundreds of grouse trails [in snow] leading to the top of the peak from the north, east, and west; none went down. Birds appeared to congregate during the day in an area of ~30 m^2 at the top of the peak. At about sunset or sunrise, most birds flew toward lower elevations to the south in flocks of 12–100 birds.

Only Anthony (1903) has described such mass spring movements, although Boag (1958, p. 17) reported seeing "grouse . . . gliding at a considerable height" onto his study area at Sheep River in May, behaviour he considered similar to spring migration as described by Anthony. Caswell (1954*b*) saw three long downward flights in March that he considered similar to those described by Anthony. In subalpine Vancouver Island, King (1971) found an easterly shift in the orientation of grouse tracks in snow, beginning ~25 March and ending ~10 April. Grouse appeared to fly onto his study area from the west, walk (up to 450 m) to the crests of slopes, then fly toward lowlands to the east—travelling "alone and in straight lines" (p. 17). At Comox Burn in early spring we have seen where grouse have flown to within a few metres of a small patch of bare ground, landed on snow and walked to the bare patch, at which point they were sometimes found. Flight direction was easterly from higher ground to the west. These observations agree with those of Anthony that downward movement in spring is principally by flying but differ in that the large flocks reported by him have not been noted by others.

(b) *Summer–autumn.* Anthony (1903, p. 26–27) suggested that autumn migration is similar to, but more gradual, than in spring, with well-grown young and adults ". . . returning as they came by walking . . . to the tops of the hills and ridges and . . . flying as near to the top of the next as their gradually descending flight will carry them."

In northcentral Washington, Wing et al. (1944, p. 430) saw groups of 3–6 males and occasional lone females moving up slope in mid July. Broods attended by one or more females, unattended broods, "bands" of chicks of more than one age, and females without chicks were seen on breeding range in late summer, prior to movement to winter range. Migrating females with broods seemed to pay little attention to their young, and the highest proportion of unattended broods was found at upper elevations. From these observations, Wing et al. suggested that most brood hens abandoned their young before reaching winter grounds. Some birds apparently moved above upper treeline and fed on grasshoppers and *Vaccinium* berries in late summer, then back down into the trees to winter.

Lone hens, sometimes in small groups, and lone or small groups of chicks unattended by hens in late summer, are indicative of brood breakup (15.3.3(h)). Breakup of at least some broods is often reported in late summer, prior to, or shortly after, departure from breeding range (Wing 1947; Bendell 1955*a*; Boag 1958; Mussehl 1960; Weber 1972; Harju 1974). Migration of brood hens and chicks, however, is not contingent on breakup, for intact broods have been monitored well into their traverse toward winter range. For example, Lance (1970) monitored a radioed hen with a radioed chick and six unmarked chicks in initial stages of migration. These birds left Comox Burn 1 September and stayed together for at least the first 2 days of travel. They covered ~10.5 km by 6 September (1.75 km/day; 0.8 km in one 6-h period), at which location the radioed birds, at least, were still together. They remained there at between 900 and 1200 m elevation until 9 October, the last location for them. Travel was directional, heading on day 6 within 2° of that on day 1. This move represented a sudden change in behaviour from occupation of a relatively small brood range in the lowlands to a relatively rapid unidirectional move toward winter range at higher elevation. Walking was the only mode of travel seen, up or down slope, and the birds moved directly through areas of dense vegetation. Lance suggested such a high rate of travel is likely sufficient to identify migratory movement. All other chicks seen near where these birds settled were with hens.

A second radioed hen with brood left Comox Burn toward winter range 3 September and 9 days later was in subalpine parkland, at ~1700 m elevation and 15 km west of their summer range (Sopuck 1979)—a mean rate of travel of 1.7 km/day. Migration began with a sudden long move toward upland forest to the southwest. Sopuck also documented rates of travel of four radioed broodless hens as 1.0, 1.2, 1.8 and 1.8 km/day, providing a mean rate of travel of 1.5 km/day for all five hens.

In autumn, King (1971) found grouse moving into and through his subalpine study area. They moved on foot; alone, in pairs, and in groups of up to at least six birds. Hens with chicks were not found with other broods. Broodless hens were almost always alone, rarely with males (three times) or other broodless hens (once), and once with a hen and chicks. Birds appeared to pass in "waves", through different areas on different days, perhaps funnelled by local topography. King thought birds first chose a direction of travel, then a route that permitted it; e.g., they would alter direction slightly to bypass a barrier such as a steep cliff and pass upward through a gully.

Hines (1986*b*) provided quantitative information on the relationship between brood breakup and autumn migration. Most juveniles (>95%; extrapolated by us from Hines's Fig. 1) at Hardwicke Island were still in intact broods in August. Some had started to disband by late August. By late September ~30% were still with hens, by mid October, <10%. Only 49% of radio-marked chicks were with known siblings in September (n = 49 contacts), none after 1 October (n = 73 contacts). Hines suggested brood breakup was likely completed there by 1 October. ". . . only a small sample of juveniles whose mothers were known were found together in fall and winter" (p. 422).

Data from Hardwicke Island seem to contrast with those for Vancouver Island with respect to brood organization during migration. However, only two radio-marked broods were monitored on Vancouver Island (Lance 1970; Sopuck 1979), both during early stages of migration. And Lance's and King's (1971) observations of other chicks with hens may not represent birds with their own mothers. We think many, if not most, broods have disbanded by the time birds have settled for winter, as indicated by Wing et al. (1944) and Hines (1986*b*).

The late PL Wright (letter, 25 September 1996) reports having twice seen very large autumn concentrations of blue grouse in some 40 years of hunting in western Montana, once in 1943 and once in 1962. He described the 1962 encounter:

> "As I approached a 10 or so acre patch of mature trees, the blue grouse started flying from the trees in singles and small flocks . . . They were wary . . . There were many birds, at the time I estimated 100."

The 1943 encounter was similar and also involved ~100 birds. Anecdotal reports of large flocks have been received from other hunters too, but none so large as above. We think such migratory flocks are composed principally of hens and chicks—not necessarily hens with their own chicks. These are likely loosely organized groups that break up before birds settle for winter, for such large flocks have not been reported on winter range.

17.1.3 Pre-breeding migration

Within migratory populations, movement from winter to breeding range is rapid (Wing 1947; King 1971) and varies among sex and age classes (Bendell 1955*a*; Zwickel 1977). Earliest spring identifications of banded birds in the four breeding sex and age classes at Comox Burn illustrate the general pattern of arrival on spring range (Fig. 17.1[2]). Adult males arrive first (mid to late March), followed shortly by yearling males and adult females (usually the first week of April). Yearling females begin arriving ~1 week later. A similar pattern was described for males and females at Middle Quinsam (Bendell and Elliott 1967), but age classes were not separated there. Boag (1964) and Weber (1975) also suggested that males arrive first on breeding range, at Sheep River and Liberty, respectively. Caswell (1954*b*) found no females until 4 days after the first males arrived on breeding range (Idaho) but thought this might reflect different conspicuousness of the sexes.

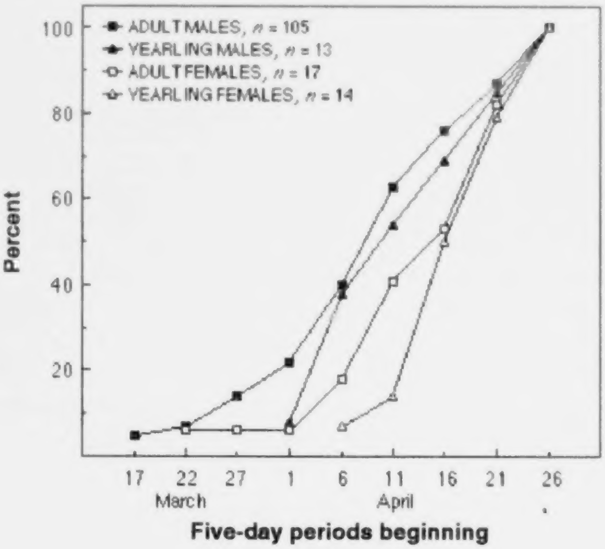
Earliest ever spring sightings of the four sex and age classes at Comox Burn were as follows: adult male, 18 March; yearling male, 1 April; adult female, 25 March; and yearling female, 9 April. A second yearling male wasn't identified until 8 April, and a second adult female, until 6 April. Yearling females weren't found in appreciable numbers until after 15 April. We believe most adult males were on breeding range at Comox Burn by end of the first week in April in most years, most yearling males and adult females by mid April, and most yearling females by 21 April. King (1971) reported that spring movement from winter range toward Comox Burn was mostly completed by mid April, as based on disappearance of birds from wintering areas, and consistent with arrival times in the lowlands.

At Hardwicke Island, "newly-arriving males" were reported on the study area in late February and early March in 1980 and 1982 (Hines 1986*a*, p. 17). These observations are confounded, however, because the island is small and relatively low in elevation, with some birds wintering on the study area. Adult females weren't recorded until the first week in April in either year. Mean date of arrival of six radio-marked yearling males was 4 April (15 March–16 April), and of eight radio-marked yearling females, 16 April (10–23 April). Except for the possible very early arrival of some males, these data are in agreement with those from Comox Burn.

In Idaho, Caswell (1954*b*) found few grouse on winter range after 26 March and estimated that spring migration lasted ~2 weeks. Weber (1975) indicated that time of spring migration at Liberty may vary among years, but his suggestion is not well documented. We suspect he is correct, but our data, too, are insufficient to show such variation.

In summary, movement from winter to breeding range is rapid, usually beginning in mid to late March, and entailing a period of 2–4 weeks for most populations studied. Most birds are alone when first found on breeding range. Although timing of spring migration is poorly documented for most populations (most field studies usually began after their arrival on breeding areas) the general pattern is clear.

Fig. 17.1. Cumulative percentages of first spring sightings of banded adults and yearlings by 5-day intervals, Comox Burn$_{cp}$, 1974–1977. Symbol for the period beginning 26 April represents 100% of initial sightings for each sex and age class, respectively, to and including 30 April.



17.1.4 Post-breeding migration

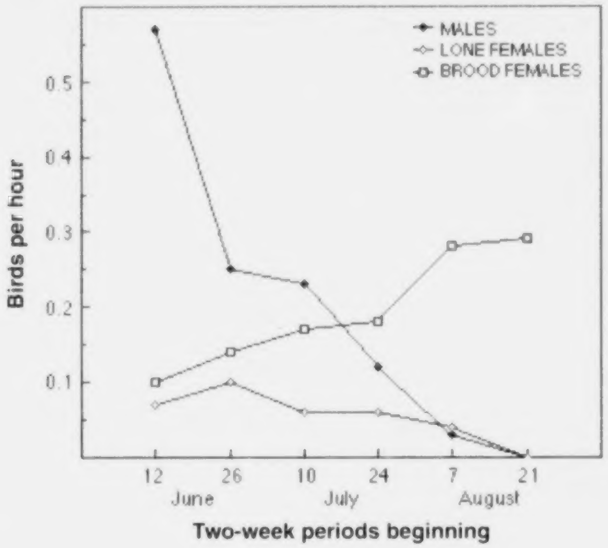
Return to winter range is much more protracted (Anthony 1903; Wing 1947) and better documented than that to breeding range. Although often referred to as autumn migration, it may begin as early as late May in some classes of birds and extend into October (Caswell 1954*b*), even November (Wing 1947; Cade 1985), in some areas.

(a) *Early observations.* Males (Wing et al. 1944; Caswell 1954*b*; Boag 1964; Weber 1975) and broodless females (Mussehl 1958; Bendell and Elliott 1967) have been reported to leave breeding range before females with broods, but early evidence of movement from breeding range was largely circumstantial.[3]

Bendell and Elliott (1967) provided data from Middle Quinsam to illustrate the pattern of movement of males, lone females, and brood females from their study plots (Fig. 17.2[4]). Most males and lone hens were gone by early August. Since adult hens are more successful than yearlings in producing broods (see 18.5.1(a)), more yearling than adult females left summer range early. Hunting season recoveries at Comox Burn and vicinity in early September were consistent with these observations. Among 258 yearling and adult females killed (most on breeding range and presumably with brood), only 20% were yearlings, significantly fewer than the mean, 39% (see Table 18.9), for birds on breeding range [1].

(b) *Evidence from radio-marked birds.* All sex and age classes of birds have been marked with radios in recent years, providing more detailed information about post-breeding migration. Among 11 yearling males monitored at Comox Burn (Sopuck 1979), mean date of departure from spring home ranges was

Fig. 17.2. Males, lone females, and brood females recorded per hour of search at Middle Quinsam by 2-week intervals, 12 June to 3 September 1960. Data extrapolated from Table 2 of Bendell and Elliott (1967); hooting and silent males combined.



18 June (3–27 June; one male not in that sample was on the study area until at least 13 July). Two that left the first week of June were on nearby subalpine ridges, ~7 km from Comox Burn, on 14 June. Among 16 yearling males monitored at Hardwicke Island, median date of movement off spring home ranges was 14 June (16 May–29 July; Jamieson 1982), but it is not clear whether all were moves toward winter range. Some may have been displacements within breeding range.

Lewis (1984*a*) monitored eight adult males on Hardwicke Island. First territorial abandonment was 17 or 18 June; the last, 11 August; seven, on or before 20 July. Three moved into conifer forest typical of winter habitat, and five, to areas typical of breeding habitat, but exhibited no territorial behaviour there.[5] The latter likely moved to winter range later, suggesting a two-staged migration.

At Middle Park, 14 males moved off breeding range and settled on "summering areas" between 24 June and 27 July (median = 7 July; Cade 1985, p. 27). One to 3 weeks were spent making these moves. Summering areas of five were 0.9–4.5 km (median = 1.8 km) from their subsequent winter ranges. Earliest arrival of 10 adult males at their winter sites was 10 October, and the latest, 21 November (median = 14 October). Cade concluded that departure from breeding areas by adult males may not result in a direct return to winter range and that their migration may be two-staged, as indicated for some males at Hardwicke Island. All males at Middle Park moved into conifer forest after leaving breeding areas (Cade and Hoffman 1993).

A principal factor affecting time of departure from breeding range for females is success or failure in producing a brood (Bendell and Elliott 1967). Mean date of departure from Comox Burn of 10 broodless hens (8 yearlings, 2 adults) was 19 July (14 June–22 August (Sopuck and Zwickel 1992)). These hens remained on breeding range for 28 days on average (3–54 days), following loss of their clutches or broods.

At Comox Burn, a yearling hen and her brood abandoned their summer home range 1 September, heading toward winter range at higher elevation (Lance 1970; see below). An adult hen with brood left toward winter range 3 September (Sopuck 1979; see below). Among five other brood hens there, two were on breeding range until at least 22 August (at which time their radio transmitters were removed), and three, until at least 1 September.[6] Collectively, data from radioed females at Comox Burn indicated that lone hens left breeding range, on average, a month or more before those with broods, while hens with chicks remained on breeding range until mid August or beyond. These observations are consistent with Bendell and Elliott's (1967) contention that few brood hens left breeding range [at Middle Quinsam] before 1 September.

At Middle Park, 13 yearling and adult females left breeding range at a median date of 15 August (25 May–30 October (Cade 1985)). Non-breeders and failed breeders left earliest, and brood females latest, but supporting data were not presented. Females departed 5–7 weeks later than males and arrived on winter home ranges at a median date of 23 October (24 September–16 November).

Hines (1986*a*) monitored movements of radio-marked juveniles between summer and winter home ranges at Hardwicke Island. Among 85 estimated departure dates, the mean was 4 October and ranged from the last week of August to the third week of November. Numbers leaving per week fit a normal curve [2], with a mode in the first week of October (calculations by us from data in Hines's Fig. 2.4). Departure was a gradual process, spread over nearly 3 months. Among six radio-marked hens, four without broods left breeding range between 10 August and 10 September; and two with broods left ~15 September and ~6 October, respectively.

In general, where data are available, hens with chicks stay on brood ranges until late summer, mid August or later. In western Montana, however, a hen with 2-week-old chicks abandoned their brood range 27 June and by 6 July had moved >8 km (mean daily moves of ~1 km/day (Mussehl and Schladweiler 1967)). Six other hens left brood ranges between 19 July and 2 August. Early moves may have been related to desiccation of herbaceous cover (Mussehl and Schladweiler 1967). These birds were on an experimental insecticide spray area, with an unusual number of human observers present for several days after the spraying. Although these disturbances were not thought to cause the early departures, they cannot be ruled out. Perhaps the experimental reduction in insect populations also contributed to an early departure of some birds?

(c) *Distances and directions moved—interpretations from band recoveries*.[7] The first detailed information on autumn migration of individuals came from hunting season band recoveries in the Bridger Mountains, MT (Mussehl 1960). Among 25 recoveries, 12 showed no change in elevation and a median distance moved of 0.8 km (0–3.4 km; calculated by us from data in Table 3 of Mussehl (1958)), from last sighting on lowland breeding range. These birds may not have begun, or may have just begun, departure from breeding range. The others had moved a median distance of 3.1 km (Table 17.1) and gained a median of 427 m in elevation from last sighting on breeding range. Most birds appear to have been banded below, and killed

Table 17.1. Distances moved, gains in elevation, and directions moved by banded grouse from breeding range toward winter range, as determined from hunting season recoveries.

Area,[a] sex–age class	n	Distance, km (range)	Elevation gain, m	Principal direction
BRIDGER MTS.				
All classes	13	3.1[b] (1.1–5.0)	122–853	10°–125°
LOWER–MIDDLE QUINSAM				
Hens and chicks	28	5.8[c] (1.6–16)	Up[d]	180°–270°
METHOW VALLEY				
All classes	22	13.7[b] (3.2–49.9)	Up	300°–40°
COMOX BURN				
All classes	40	5.7[b] (1.5–28.5)	Up	200°–310°

Note: Includes only birds considered as en route to, or on, winter range when killed.

[a] Sources: Bridger Mts, Mussehl (1960); Lower–Middle Quinsam, Bendell and Elliott (1967); Methow Valley, Zwickel et al. (1968); Comox Burn, this study.

[b] Median distance.

[c] Mean distance.

[d] Virtually all birds moved up but locations not precise enough to determine elevations.

above, 1700 m; one at ~2400 m (Fig. 6 in Mussehl 1960). Directions of travel were almost all northeasterly, toward the nearest winter habitat. All birds but one were shot in September, so some may have still been en route to winter range.

Bendell and Elliott (1967) reported on 55 autumn hunting season recoveries of birds banded at Lower Quinsam ($n = 6$) and Middle Quinsam—three were adult males, the rest hens and chicks.[8] Based on distances moved, 51% were classified as migrating (moves >1.6 km). Those considered in transit had moved a mean distance of 5.8 km (Table 17.1); 61% had gone 1.6–3.2 km, 39% >3.2–16 km. Although birds went in most directions of the compass, the majority travelled southwesterly, toward nearby upland forests. Most (80%) were last seen on breeding range in July or August, were shot by mid September, and some may have still been en route to winter range.

Recoveries of birds banded on or adjacent to the mainly shrub-steppe Methow Game Range show some of the longest moves. Here, among 30 recoveries from hunters, three indicated no movement from point of banding, and five, moves of ~1.6 km (data in Zwickel et al. 1968). Distances did not differ among sex and age classes or between birds recovered directly or indirectly [3], so these data were combined. Median distance moved by birds considered in transit to, or on, winter range (moves >1.6 km) was 13.7 km (Table 17.1). Most were banded under, and killed at over, 1000 m elevation, some at >1500 m, in areas that would be mainly in Douglas-fir or spruce–fir communities. The longest recovery distance was 50 km, a juvenile female. This very long move may represent, in part, the fall phase of natal dispersal. Among six yearling and adult females, one was killed 35 km, two 29 km, one 18 km, and two 8 km from where banded. Three males marked as juveniles and killed as yearlings or adults were 5, 6, and 13 km from where banded, significantly less than yearling and adult females [4]. Among all recoveries, 50% were more than 8 km, and 30% more than 16 km, from where birds were marked (Zwickel et al. 1968). Winter range could have been reached within ~2 km of banding locations in all cases (Zwickel 1992).

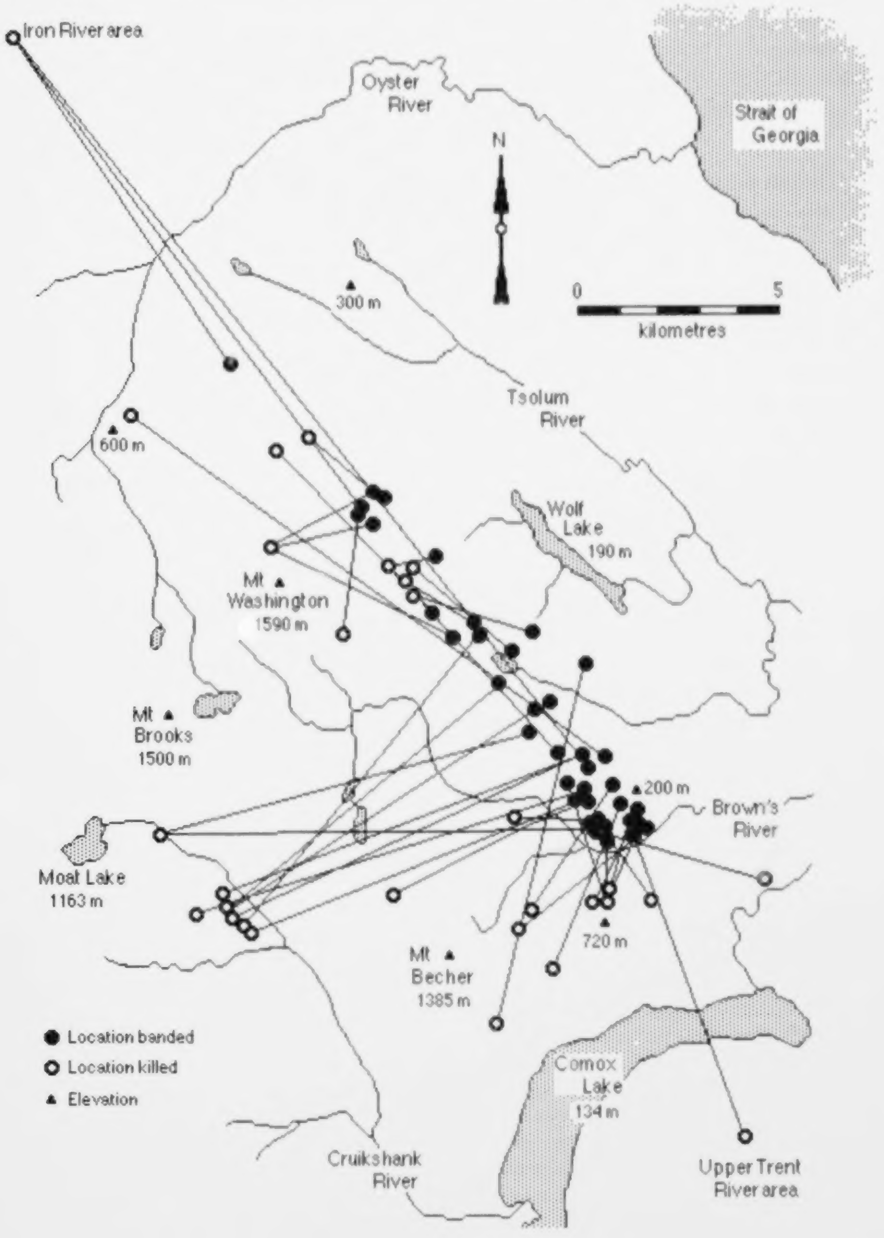
Movements indicated by recoveries in the Methow Valley were strongly directional (Table 17.1), with grouse marked near the south end of the study area travelling mainly north–northeasterly. Those banded farther north tended to move north–northwesterly, most having crossed the valley floor of the Chewack River (~600 m elevation) and gained elevations above those where marked when killed. Most did not move into the nearest available winter habitat and, as a group, spread out over an area some 25 times the size of area within which they were banded (Zwickel et al. 1968). Some grouse in Middle Park also passed through apparently suitable winter habitat en route to wintering areas (Cade 1985).

The largest sample of hunting season recoveries is from Comox Burn and vicinity; $n = 573$, 1963–1981. Season openings were all in late August or early September, with most birds taken on the first weekend of the season. Among all recoveries, 102 kill locations were too imprecise to use in analyses of movements. Among the remainder, 417 were taken while on or very near sites where banded (still on breeding range) and considered not yet en route to winter range, or just beginning their departure. The others ($n = 54$) were considered as en route to, or on, winter home ranges on the basis of distances moved from last sighting on summer range, marked changes in elevation, or both. Among the latter for which sex and age were known, 11 were yearling or adult males, 29 were yearling or adult females, and 7 were juveniles (3 males, 4 females).

Locations of kill for 40 of the latter birds were sufficiently precise to identify distances moved and routes of movement (Fig. 17.3). There were no differences in distances moved among sex and age classes or between birds recovered directly or indirectly, so these data were combined, with a median for all birds of 5.7 km (Table 17.1). All but five were killed as yearlings or adults, birds that had presumably established summer home ranges.

Distances moved by birds killed as yearlings or adults differed among the months August to November [5a]. Those of birds taken in August and September did not differ from each

Fig. 17.3. Locations of banding and hunting season recoveries of grouse marked at Comox Burn.


Iron River area
Oyster River
Strait of Georgia
N
0
5
kilometres
300 m
Tsolum River
600 m
Wolf Lake
190 m
Mt Washington
1590 m
Mt Brooks
1500 m
200 m
Brown's River
Moat Lake
1163 m
720 m
Mt Becher
1385 m
● Location banded
○ Location killed
▲ Elevation
Comox Lake
134 m
Cruikshank River
Upper Trent River area

other [5b], nor did those taken in October differ from those in November [5c]. Twenty-one killed in August and September had moved a median of 4.5 km (1.5–11.5 km); 11 killed in October and November, a median of 11.3 km (2.5–28.5 km), a significant difference between periods [5d]. Clearly many taken in August and September were still en route to winter range, while many, if not most, taken later may have been settled for winter. Distances moved by males ($n = 5$) and females ($n = 15$) in August and September did not differ [6a], but those from October and November did differ: males ($n = 4$), median = 14.9 km, 11.3–28.5 km; females ($n = 7$), median = 3.8 km, 1.5–11.4 km [6b]. Although the latter samples suggest males may winter farther from breeding range than females, this difference may reflect the later departure of females from breeding range, which seems likely.

Routes of travel of birds from Comox Burn were virtually all westerly or southwesterly (Table 17.1; Fig. 17.3[9]). As indicated by other studies, these moves were toward nearby upland forests, beyond the lowland clear-cuts on which they had summered. All birds but one juvenile male were killed at elevations above where they had summered.

(d) *Distances and directions moved—interpretations from radio-marked birds.* As noted above (17.1.4(b)), two yearling males left Comox Burn the first week of June and were in subalpine parkland 1 week later, ~7 km from their spring ranges (Sopuck 1979). Median distance between breeding and wintering areas of 11 males at Middle Park was 10.6 km (Table 17.2), and median gain in elevation, 450 m. Among nine "long-distance" migrant males there (moves ≥3 km), six went east–northeasterly, one easterly, and three southerly (calculated by us from Cade's Fig. 4). All wintered at higher elevations than birds that remained on study areas (Cade and Hoffman 1993).

The median straight-line distance from summer to winter home ranges of 10 broodless hens (8 yearlings, 2 adults) at Comox Burn was 4.3 km (Table 17.2), and the median elevation attained, 991 m (914–1981 m). Migration was initiated by a sudden, directional move to the west or southwest. Two found more than once exhibited strongly unidirectional travel. They moved 7 and 14 km, respectively, were found in the same locations 2 weeks later, and likely had settled for winter.

At Middle Park, median distance between breeding and wintering ranges of 19 females was 1.2 km (Table 17.2), and median gain in elevation, 120 m, both significantly less than for males. Among six "long-distance" migrant females, three moved east–northeasterly, and three, southerly (calculated by us from Cade's Fig. 4). Median distance moved and elevational change of seven juvenile females (Table 17.2) did not differ from those of adult females (Cade and Hoffman 1993). Moves of <3 km between breeding and wintering ranges were less directional, some of which did not extend beyond the study areas and might be classified as non-migratory.[10] Some of these birds may have done little more than shift from shrub-steppe habitat in summer to "islands" of conifers surrounded by shrub-steppe for winter. Nevertheless, birds occupying <10 km^2 in spring and summer were spread over an area >400 km^2 in winter (Cade and Hoffman 1993).

Table 17.2. Distances moved and gains or losses in elevation by birds equipped with radios on breeding range and monitored en route to, or to, winter home ranges.

Area,[a] sex–age class	*n*	Median distance, km (range)	Elevation gain/loss, m
MIDDLE PARK			
Male	11	10.6 (1–29.5)	200–600
Yearling–adult female	19	1.2 (0.1–28)	0–760
Juvenile females	7	0.6 (0.1–5.4)	0–360
COMOX BURN			
Broodless females	10	4.3 (1.0–20)	300–1700[b]
HARDWICKE ISLAND			
Juvenile males	34	1.9 (0.0–12.0)	—
Juvenile females	76	2.3 (0.0–15.0)	—
MILLER RIDGE			
Adults and juveniles	73[c]	1.6[d] (0.4–11.9)	–308–403

[a] Sources: Middle Park: Cade (1985), Cade and Hoffman (1993); Comox Burn: Sopuck and Zwickel (1992); Hardwicke Island: Hines (1986*a*); Miller Ridge: Pelren (1997).

[b] Estimated by us from data provided by L. Sopuck.

[c] 48 adults plus 24 juveniles.

[d] Mean distance.

Movements of juveniles to winter ranges on Hardwicke Island were variable (Hines 1986*a*), with some remaining on or near their summer ranges, others moving relatively long distances; 28 of 110 (25%) moved >5 km, and 7 (6%), >10 km. At least seven (three males, four females) flew to the mainland, a flight of at least 350 m across open water. Median moves of 1.9 km by males and 2.3 km by females (Table 17.2) did not differ between the sexes.[11]

Among 72 juveniles that moved <5 km at Hardwicke Island, directions were "essentially random" (Hines 1986*a*, p. 17). Moves >5 km were highly directional and easterly (calculated by us from data in Hines's Fig. 2.1). This partly reflects configuration of the island[12] but also led to higher elevations and the more extensive older second-growth and old-growth forest present there. As with data from hunting season recoveries, migratory patterns of juveniles cannot be determined until they have established summer and winter home ranges as yearlings.

Pelren (1997) radio-marked grouse on Miller Ridge, where forest, parkland (open forest and grassland), and grassland were distributed as a mosaic. Forested communities were mainly on north-facing slopes, and grassland, on south-facing slopes. Potential winter habitat, forest and parkland, was intermixed with potential breeding habitat, principally parkland and grassland. Distances between summer and winter ranges did not differ between juveniles and adults, between sexes, or among years and were generally short compared to results from other studies (Table 17.2). Some adults remained on their summer home ranges throughout winter, but all juveniles moved >0.4 km to winter sites. Short movements likely reflected the close proximity of breeding to winter habitat found there. Changes in elevation were slight, generally less than 100 m, with some individuals moving down for winter (Table 17.2). Small and downward elevational changes likely reflected the relatively high elevation of the study area as compared to surrounding terrain.

17.1.5 Ultimate stimulus for migration

Blue grouse appear to be obligate, or near-obligate, conifer feeders in winter (see 12.1.2)—likely reflecting a historical trophic requirement. All evidence indicates females feed heavily, though not exclusively (Zwickel and Bendell 1972*b*; King and Bendell 1982), on non-coniferous foods in spring and summer, up to at least the time of post-breeding migration. Chicks also use conifers only lightly prior to departure from breeding range (Beer 1943; King and Bendell 1982). Movement from winter range to shrub-steppe, subalpine forest, or open coastal or montane forest in spring strongly suggests a requirement of hens and chicks for non-coniferous foods, those often not readily available in forest. The ultimate stimulus for migration in blue grouse is likely this adaptation to different habitats for breeding and wintering, an adaptation most likely driven by the needs of hens and chicks.[13] We know little about physiological adaptations to these different seasonal habitats except that energetic constraints on blue grouse in winter appear minimal (Pekins 1988), and the observation that this grouse breeds and winters under a wide range of climatological conditions—cool and wet to hot and dry in breeding season and mild and wet to cold and dry in winter. (7.2.2).

17.1.6 Proximate stimuli for migration

(a) *Pre-breeding migration.* Proximate stimuli for spring migration have not been studied, but there is speculation based on general observations (Weber 1975; Zwickel 1992). Gonadal development is underway in at least adult and yearling males and adult females at time of arrival on breeding range (data in Hannon et al. 1979 and Standing 1960), but not clearly so in yearling females (see 10.3.1). Thus, spring migration is probably hormonally mediated (Zwickel 1992), likely triggered in part by photoperiod. If spring migration is related to day length, however, its timing may be modified by local phenology, for there is no clear relationship between breeding events and latitude (see 10.2.2(a)). In some areas, birds arrive on breeding range as the ground clears of snow, providing access to ground-level vegetation (Weber 1975). But this cannot be a universal stimulus because many birds, especially in coastal areas, breed in lowlands with little or no snow in winter. Also, those that breed in subalpine habitat may begin courtship activities in areas with >1 m of snow and virtually no snow-free ground (pers. observ.), in some years, even in coastal lowlands (Fig. 17.4). Nevertheless, late snow cover in lowland areas might delay spring movement onto spring–summer home ranges.

New plant growth might be a trigger for spring migration. But this too cannot be a universal stimulus, for breeding behaviour of males was well underway at our subalpine study area at Hudson Bay Mt. before new growth was available, likely a common situation in subalpine areas.

(b) *Post-breeding migration.* Factors initiating departure from breeding range must differ among males, unsuccessful or non-breeding females, and broods, with, in all likelihood, differences between hens with chicks, those dissociated from their chicks, and unaccompanied chicks.

Little is known about what might initiate post-breeding departure in males and broodless females except to note that it generally coincides with gonadal regression (data in Hannon et al. 1979). Most yearling and adult males desert breeding range over a period of a month or less, beginning about mid June at Comox Burn, shortly after chicks begin to hatch. Rarely, yearling males, and occasionally adult males, remained in breeding habitats at Comox Burn and Hardwicke Island as late as early August. Most males also leave interior breeding ranges by mid July (Harju 1974; Weber 1975; pers. observ.).

Among females that lose nests or broods some leave shortly after such loss, others later (17.1.4(b)). The only constants are that they leave following loss, and, on average, earlier than hens with broods or chicks themselves. Most males and broodless hens abandon breeding ranges during peak vegetative growth and fruit production.

Migration of brood hens and (or) their chicks has received most attention. Some early workers suggested that post-breeding migration is a response to depletion of berries in the lowlands and their ripening in the uplands (Beer 1943; Marshall 1946). Musschl (1960) found a correlation between depletion of berries and departure in one year, but not in another. He suggested an abundance of low red huckleberries (*Vaccinium scoparium*) at upper elevations may affect local distribution, but only after migration has begun. Others have noted that migration begins before a depletion of fruits in breeding areas (Fowle 1944; Caswell 1954*b*; Henderson 1960; Musschl 1960; Bauer 1962; Harju 1974) or that berries and (or) insects are more abundant on lowland ranges than in the uplands when departure begins (Heebner 1956). We doubt that availability of fruits is an important initiator of migration or that it is likely to alter the schedule greatly, as also suggested by Bendell and Elliott (1967).

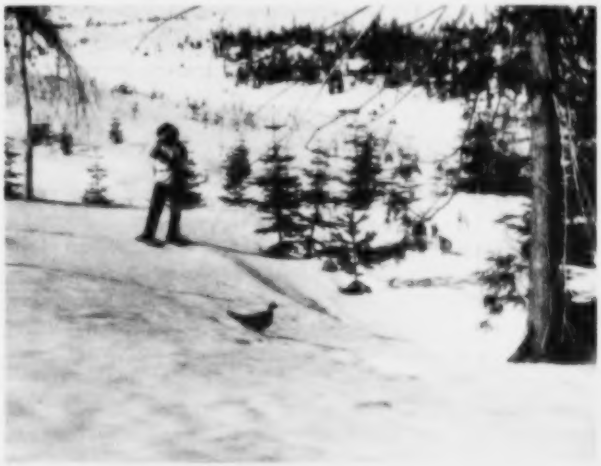


Fig. 17.4. In 1975 heavy snow pack covered most of Tsolum Main in early April, when adult males returned to breeding areas.

Desiccation of vegetation in late summer can affect food plants and cover and has been proposed as a proximate stimulus to migrate (Bendell 1954; Henderson 1960; Musschl 1963*b*; Pelren 1997). Bendell (p. 89) postulated that early migration from Lower Quinsam in 1951 and 1952 may have been related to desiccation of plants, and from this, that weather ". . . through its effect on food [and] vegetation conditions the altitudinal migration of hens with young." Henderson thought desiccation of plants may have caused early migration of broods at Frazer Creek in 1958—late-summer censuses there indicated its initiation can vary by 2–3 weeks among years. Neither depletion of fruits nor desiccation of vegetation explains why movement of hens with broods from breeding range may span a 2–3 month period, however.

Fowle (1944) felt that any relationship between depletion of berries and migration of hens and young may be accidental and Harju (1974, p. 107), that it may be "largely circumstantial and irrelevant". We think the stimulus for post-breeding migration is more fundamental than can be explained by depletion or desiccation of food (including fruits) and cover but that either might advance its start in extremely dry years.

In some areas, post-breeding migration begins when maternal bonds are weakening, as indicated by brood breakup (Wing et al. 1944; Bendell 1955*a*; Musschl 1960; Bauer 1962; Zwickel et al. 1968; Hines 1986*b*). As noted above, however, some chicks stay with their mothers during at least its initial stages, so disintegration of broods is not necessary to initiate this movement. Buss (1960) and Henderson (1960) thought age and (or) growth and physiology of chicks may be involved. On Hardwicke Island, however, Hines (1986*a*) found no relation between date of hatch and time of departure from breeding range of 85 radio-marked chicks—they began to move at 65–155 days of age (mean = 114). Age alone will not explain these moves, although some threshold age may have to pass for them to begin.

Post-breeding migration may reflect an innate behavioural pattern (Henderson 1960; Bauer 1962; Harju 1974), an evolutionary adaptation to the environment (Buss 1960). In adults it involves a return to previous winter range, but in juveniles it likely involves a tendency to both migrate and disperse. Its control is likely physiological in nature, perhaps in part a response to shortening day lengths (Heebner 1956; Henderson 1960; Harju 1974), and may be modified by external factors, e.g., weather and vegetation. The stimulus, or stimuli, causing particular individuals or broods to initiate post-breeding movements appear complex, however, as evidenced by variations in dates of departure within sex and age classes. Questions remain as to why some broods disband prior to or during migration, while others remain intact during at least its initial stages, and why there is such variation in relation to age of chicks. The impulse to move seems strong in most individuals, for once begun, travel appears rapid and highly directional.

17.2 Dispersal[14] and site fidelity

> *The dispersal of a species is primarily accomplished in the immature stages. . . Once a bird has reached sexual maturity and nested, it has strong tendencies to return to the same area in following years.*
>
> SC Kendeigh (1974)

In its broadest sense dispersal represents a movement or scattering away from an area and in this context might include migration. Among vertebrate biologists it is frequently used to signify a more or less permanent move that most often involves immature individuals seeking a place to settle, so-called "natal dispersal" (Greenwood 1980). In this context, it is a move from where an individual is born to where it will breed, or attempt to breed (Johnston 1961; Payne 1990). Movement of breeding sites by older birds represents "breeding dispersal", and a change in winter home ranges between or among years might be considered "winter dispersal". We consider dispersal and migration as separate phenomena because of the differing functions they serve, but among first-year birds, at least, they are not completely separable.

Dispersal has a number of potential consequences, among which are genetic mixing, colonization of occupied and vacant habitats, impacts on populations from which individuals move, or join, and risks to survival as animals traverse unfamiliar terrain. It may be innate or environmentally induced (Howard 1960), vary by sex and age (Greenwood 1980), and, ultimately, be driven by such things as avoidance of inbreeding, competition for mates, and competition for resources (Dobson and Jones 1985). It likely reflects in part an innate drive, with the home range within which an individual settles determined by its own attributes, available habitat, and interactions with conspecifics and other organisms.

17.2.1 Natal dispersal

Movement from natal area to breeding area in blue grouse usually is not direct and involves a winter sojourn at a third and separate site. Distances to winter range by juveniles likely exceed those classified as natal dispersal in most cases and may involve what might be called "dispersive wandering" as young birds search for a suitable winter area, the autumn phase of dispersal (Schroeder 1985). Only Hines (1986*c*) has examined autumn and winter movements of juvenile blue grouse, as they might affect natal dispersal. He found wide variations among individuals and concluded (p. 143), "dispersal was a complex process not easily attributed to a particular time of year or a particular type of movement pattern." We do not know what influence first-winter site might have on choice of breeding site but suspect spring return to, and search on, breeding areas, the spring phase of dispersal (Schroeder 1985), is most relevant in determining where a young bird settles for breeding.

Prior to our studies at Comox Burn and Hardwicke Island, there were few data on natal dispersal distances for blue grouse. Mussehl (1963*b*) reported on two birds marked as juveniles in western Montana. A male was found, in August of its second year, 9.7 km from where banded the year before. This cannot, however, be considered a natal dispersal distance, for by August, most yearling and adult males have returned, or are en route, to winter range. Secondly, a yearling female with nest was 2.6 km from where banded on breeding range the previous year. Having found few returns of juveniles to his study areas, Mussehl suggested most disperse from natal areas. At Sheep River, Boag (1966) documented a natal dispersal move of 6.4 km by a female. Bendell and Elliott (1967) reported on five likely natal dispersal moves at Middle Quinsam. Two males were found on breeding range in years subsequent to banding, 0.7 and 2.1 km from where banded as juveniles. Three females were 1.0, 1.8, and 2.4 km from where banded as juveniles.

Intensive marking of juveniles at Comox Burn has provided better samples for an analysis of natal dispersal.[15] A summary for birds marked on our control plot, Comox Burn$_{cp}$, was provided elsewhere (Jamieson and Zwickel 1983*a*), and we now examine data for birds marked on the entire area.[15]

Distances moved between marking as juveniles and locations on breeding range as yearlings or adults (Table 17.3[16]) did not differ within sexes, so age classes were combined. In all cases, distances moved by males were significantly less than those of females [7a–c]. Moves by "all" males and "all" females were essentially the same as reported earlier for the control plot. Among males, 68% dispersed less than the median distance for females, but only 31% of females dispersed less than the median for males, a clear difference between sexes [8] (see also Fig. 17.5). The longest possible natal dispersal distance at Comox Burn, 12.1 km, was for a brood female, but this move was not included in the above analyses because she was found in July and may have already moved from her nesting range.

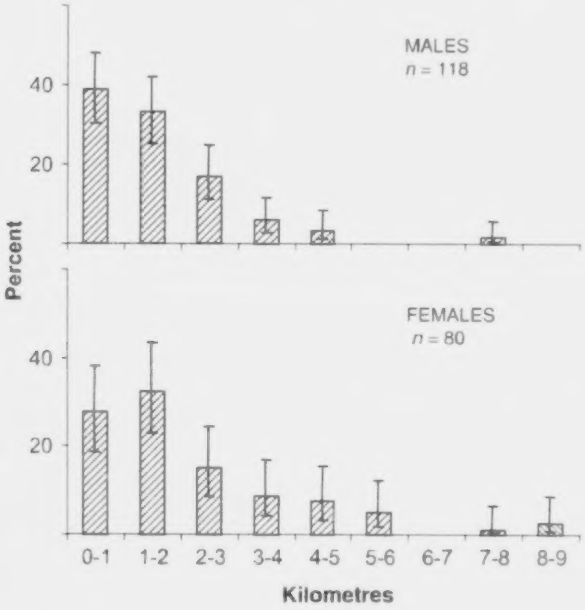
Natal dispersal of radio-marked juveniles was studied at Hardwicke Island from 1979 to 1983 (Hines 1986*c*). Medians and ranges reported for males and females were 0.9 km (0.2–2.6 km, $n = 24$) and 1.4 km (0.3–11.0 km, $n = 42$), respectively, slightly less than at Comox Burn, but likely not significantly so.[11] We examined natal dispersal distances for 22 sibling pairs banded at Comox Burn and vicinity. Male:male sibs may have settled closer to one another than female:female or male:female sibs (Table 17.4), but differences were not sig-

Table 17.3. Natal dispersal distances for grouse marked as juveniles at Comox Burn and vicinity, 1969–1978.

		Distance (km)		
Sex, age	*n*	Median	Mean ± SE	Range
MALES				
Yearling	72	1.2	1.5±0.16	0.04–8.1
Adult	77	1.1	1.6±0.16	0.1–7.6
All[a]	119	1.2	1.6±0.12	0.1–7.6
FEMALES				
Yearling	53	1.5	2.0±0.21	0.1–7.5
Adult	39	1.9	2.5±0.34	0.2–8.8
All[a]	80	1.8	2.3±0.21	0.1–8.8

[a] "All" represents all individuals, some of which are included in both yearling and adult years. Data for individuals were averaged across all years identified. If data for both yearling and adult years were available for an individual only those for adult years were used to compute "All" means.

Fig. 17.5. Natal dispersal distances of chicks banded at Comox Burn, in percent, by 1-km intervals, 1969–1979.



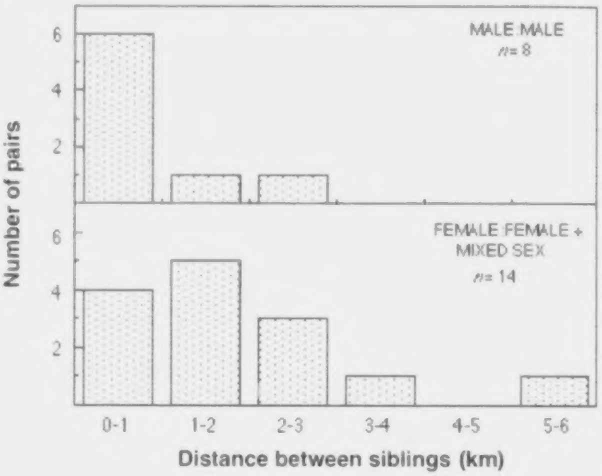
nificant [9], perhaps because of small samples. Significantly more male:male sibs settled <1 km apart than female:female and male:female sibs combined (Fig. 17.6) [10], with the latter not different.

Samples of sibling pairs are constrained because most instances found were confined to within our two main study areas.[15] Although this constraint makes an attempt to detect directionality difficult, it seems clear that individuals might settle in almost any direction from where marked relative to their broodmates (Fig. 17.7).

Table 17.4. Distances marked siblings settled apart from one another as yearlings or adults, Comox Burn, 1969–1978.

Sexes of		Distance (km)			
sibling pairs	n_{pairs}	Median	Mean ± SE	Range	*n* <1 km
Male:male	8	0.9	1.2±0.28	0.7–3.0	6
Female:female	7	1.2	2.0±0.68	0.6–5.8	2
Male:female	7	1.4	1.8±0.46	0.3–3.7	2

Fig. 17.6. Distance (km) between sibling settling locations (as yearlings or adults) of juveniles banded on breeding range for male:male and female:female plus mixed sex pairs of broodmates, Comox Burn, 1969–1979.



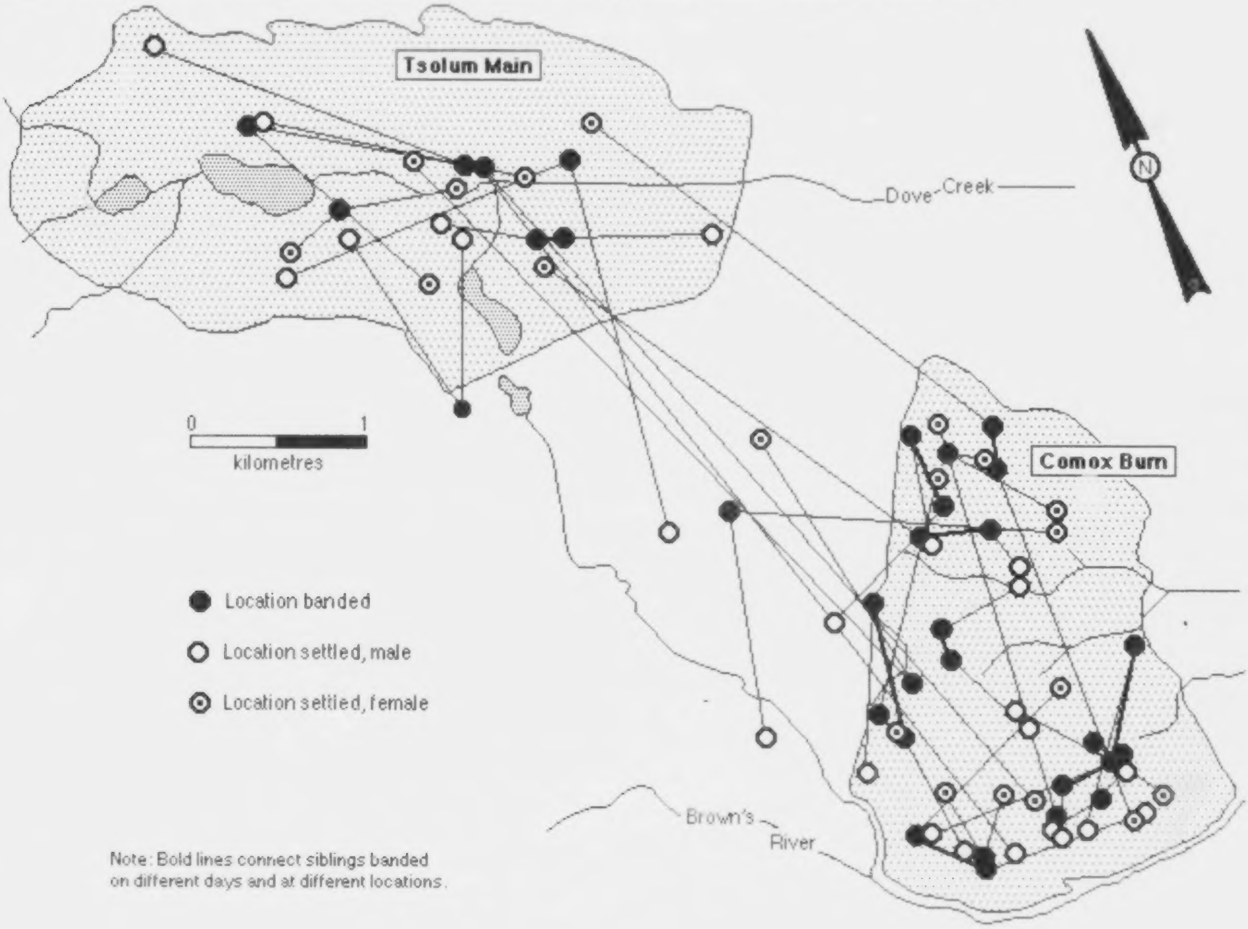
17.2.2 Breeding dispersal and site fidelity

As defined above, we use breeding dispersal to refer to a change in place of breeding between or among years, and in this sense, its converse is site fidelity.[17] The question becomes, do yearling and adult males and females exhibit breeding dispersal and, if so, to what extent?

(a) *Territorial males*. Once territorial, adult males show strong attachment to particular sites among years, as first demonstrated at Lower Quinsam (Bendell 1955*a*). Later, Bendell and Elliott (1967) reported that 133 territorial males returned to the same sites from year to year at Lower and Middle Quinsam (data combined). Two males banded in 1951 and 1952 were found in 1957 on the same territories on which they were first captured even though ". . . the forest had grown up around them" (p. 23). Similar fidelity has been reported for territorial males in Alberta (Boag 1966), Montana (Schladweiler 1968), Wyoming (Harju 1974), and Colorado (Hoffman 1981).

Minor territorial boundary shifts have been reported (Harju 1974; Hoffman 1981) and, rarely, short site changes, by territorial males. Schladweiler (1968) found that 41 of 44 males returned to territories they occupied in the previous year, 3 to adjacent territories. Over a 10-year period at Comox Burn, 23 adult males shifted territories, about 2 per year, among ~63 present each year (Lewis and Zwickel 1980). There, McNicholl (1978) examined territorial behaviour of 21 males in some detail from 1972 to 1974. Among 35 returns from one

Fig. 17.7. Map showing banding and natal dispersal locations of sibling pairs at Comox Burn$_{cp}$ and Tsolum Main.



Note: Bold lines connect siblings banded on different days and at different locations.

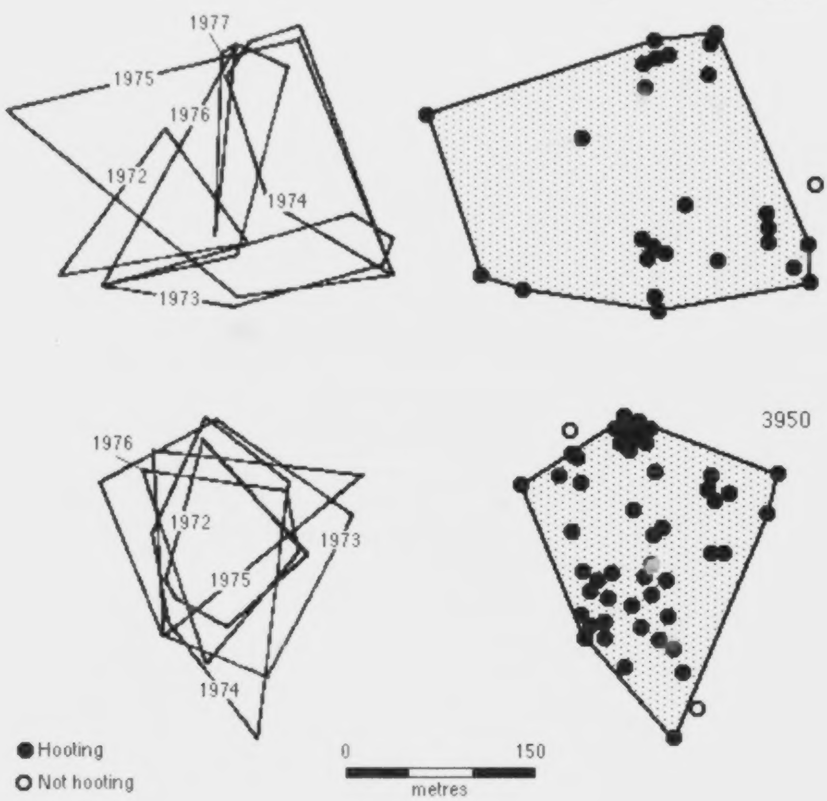
year to the next, 34 were to the same sites occupied the previous year (with two minor shifts in boundaries). Only one bird changed sites, from one side of an alder bog in year 1 to the other side the next, a move of ~100 m that may have resulted from displacement by a male that occupied his original territory in year 2. Typical adult male philopatry, illustrated by two males with 5- and 6-year territorial histories and several identifications each year, are depicted in Fig. 17.8.[18] Both had first taken these territories as 2-year-olds, and all identifications of these birds as adults are shown.

In 14 years of intense monitoring of birds at Comox Burn, we know of only one substantial territorial shift by a banded male. This bird was identified on the same territory in 1971, 1972, and 1973. He was not seen in 1974 but was hooting and recaptured in 1975, ~2 km from his original territory. One leg showed signs of injury (now healed) and may have caused his loss of territory. This is the only substantial territorial shift of which we are aware from any study. We conclude, site changes by territorial males are rare and significant boundary shifts are uncommon. Territorial males are strongly philopatric.

(b) *Non-territorial adult males*. Some adult males do not hold territories (Lewis and Zwickel 1980; Lewis 1984*b*). For example, male 939 (Fig. 17.9) was banded as a hooting adult at Comox burn in 1962 and was identified once more that year, >800 m from where banded. His seven identifications in 1963 showed moves of 277–1175 m between sequential locations, at two of which he was hooting. In 1964, at ≥4 years of age, he gained a territory, with a maximum recorded extent between any two sightings of ~160 m. He had visited this site at least once in 1963. He was hooting at five of six positions sighted in 1964 and held that territory through 1966, the last year seen. His hooting in 1962 and 1963 was perhaps an attempt to obtain a territory. Contrast 939 with the birds in Fig. 17.8, the normal situation.

It is difficult to estimate how many non-territorial adult males might be present on breeding range.[19] For example, a male taken as a replacement for a removed territorial male at Comox Burn in 1978 was banded there in 1975, at ≥2 years of age, but hadn't been identified in the intervening period. At Hardwicke Island, on a study area with 28 territorial males in 1980 and 25 in 1981, four and two banded adult males were considered non-territorial in the 2 years, respectively (Lewis 1984*b*). Three, each with 3–8 sightings, ranged over areas encompassing 3–4 occupied territories. Among 10 radio-marked as yearlings, 4 were non-territorial as 2-year-olds (Jamieson and Zwickel 1983*b*). Non-territorial adult males may not be uncommon in coastal British Columbia (Lewis

Fig. 17.8. Areas within which two adult males were observed each year (*left*) and over the entire period, 1972–1977 (stippled), Comox Burn$_{cp}$. Total identifications for 3931 is 33, for 3950 is 56. All identifications of these birds are shown.



1984*b*). A limited amount of information suggests if such birds eventually take territories, they do so within the home ranges they occupied when non-territorial (Jamieson and Zwickel 1983*b*; Lewis 1984*b*; bird 939, above). They too show strong fidelity to site.

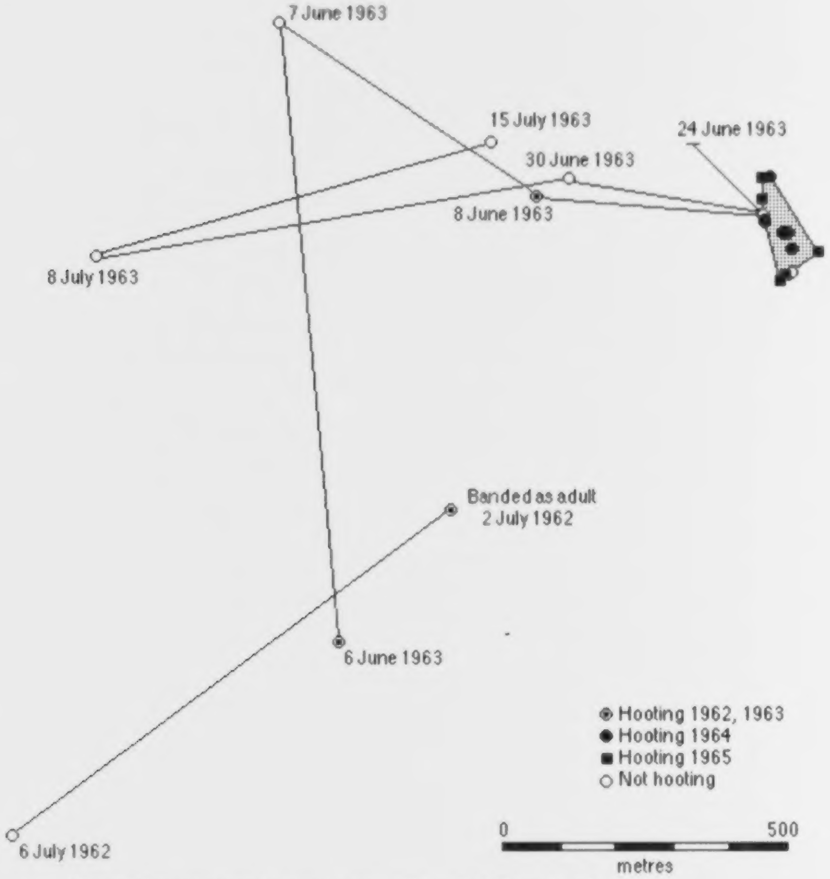
(c) *Yearling males*. Relative to adult males, yearling males are secretive on breeding range (Zwickel and Bendell 1967*b*) and are often found under logs, [small] trees (Bendell and Elliott 1967) or shrubs, or in thickets (Jamieson 1982, 1985). Bendell and Elliott reported that they moved widely, but more recent studies suggest this is only partly true. At both Comox Burn (Sopuck 1979) and Hardwicke Island (Jamieson 1982), radio-marked yearling males tended to become more localized as the breeding season progressed. Localization on breeding range appears to mark the end of the spring phase of natal dispersal.

Among 30 radio-marked yearling males at Comox Burn, 57% were classified as "localized"[20] and 43% as "wide-moving", but with a gradient between the two groups (Sopuck 1979). At Hardwicke Island, individual yearlings tended to associate with particular territories of adult males (up to six associations per yearling) or to move more widely, with no clear connection with other birds (Jamieson and Zwickel 1983*b*). Virtually all[21] had relatively restricted home ranges within which they could become familiar with the local habitat and established conspecifics.

Most yearling males appear to take territories as adults near or within the limits of their yearling home ranges (Sopuck 1979; Jamieson and Zwickel 1983*a*, *b*). For example, among 65 yearlings at Comox Burn that attained territories as adults, all territories but one were within 1.4 km of where the bird was captured or first sighted as a yearling, with a median distance of 0.3 km (0–3.7 km) between these locations and subsequent territories (Jamieson and Zwickel 1983*a*). The extreme, perhaps aberrant, 3.7 km move from yearling to adult home range was the only clear exception to this pattern. At Hardwicke Island, 6 of 11 radio-marked yearlings established territories (as 2-year-olds) on territories of males with which they had associated the year before (Jamieson and Zwickel 1983*b*), four were non-territorial as 2-year-olds, and one was killed by a predator prior to determination of its home range as an adult. Returns of 11 yearlings to where they established territories as adults (Fig. 17.10[22]) illustrate the general pattern. Maximum distance between any two locations of an individual yearling was 1.6 km. In Montana, territories of eight adult males banded as yearlings were all ≤1 km from where first captured (Musschl and Schladweiler 1967; Schladweiler 1968).

We conclude that (1) yearling males occupy home ranges large enough to familiarize them with several potential territories, (2) as adults they show high fidelity to areas occupied as yearlings, and (3) dispersal between yearling and adult years is

Fig. 17.9. Locations of male 939 as a non-territorial adult, 1962 and 1963, and as a territorial adult, 1964 and 1965, Comox Burn$_{cp}$. Stippled polygon includes all 1964 and 1965 sightings.



1964 sightings range from 8 May to 24 June; 1965, from 10 May to 21 July

rare. Although yearlings occupy larger areas than adult males, part of which reflects the spring phase of natal dispersal, virtually all settle as adults within the bounds of their yearling home ranges.

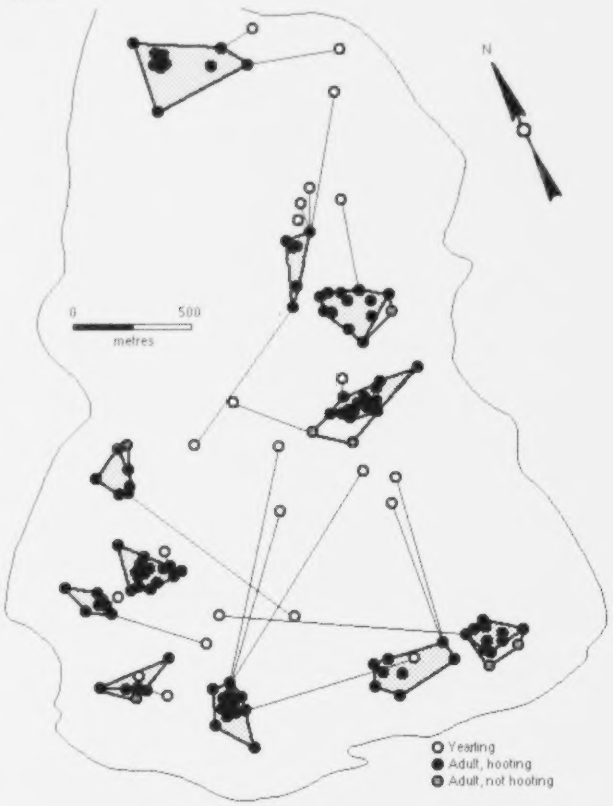
(d) *Females.* High rates of survival of females (see 18.4.2) are based mainly on reidentification of banded females, principally on study areas where marked. These data suggest females tend to return to the same general breeding area from year to year. Other data provide more precise information on fidelity.

Return to breeding range of females is more difficult to document than for adult males because of their wider movements (Bendell and Elliot 1967) and more secretive pre-hatch behaviour. Nevertheless, some authors have suggested females show high fidelity to spring home ranges (Boag 1964, 1966; Bendell and Elliott 1967; Schladweiler 1968) or brood ranges (Mussehl and Schladweiler 1967), based on reobservations of banded or radio-marked birds.

At Comox Burn, early work indicated that the median distance from breeding site as a yearling female to that as an adult was 0.4 km, while that between year-to-year breeding sites of adults was 0.2 km (Jamieson and Zwickel 1983*a*). We expanded this analysis by combining data from Comox Burn with those from Hardwicke Island.[23] These data show a median distance moved from yearling to adult years of 0.3 km (0.04–2.5 km, $n = 57$), and for adult to adult years, 0.2 km (0.03–1.9 km, $n = 79$), not quite significantly different [11], and similar to results of the earlier analysis. The tendency for greater movements from yearling to adult breeding sites may reflect wider movements of yearlings as they first sought a place to settle. Over 45% of the year-to-year breeding sites of individuals were <200 m apart, and >70% <400 m apart (Fig. 17.11), generally within the limits of summer home ranges of females. Some of the longer distances may reflect movements of birds that did not breed, or were unsuccessful breeders that abandoned localized breeding ranges. These data indicate most females return to areas of familiarity from year to year.

Nest site provides the best indicator of a female's spring breeding range, but samples for known females with more than one nest are relatively small. Among 31 banded females for which we located two or three nests at Comox Burn and Hardwicke Island, the median distance between (1) yearling and adult nests was 155 m (57–1945 m, $n = 12$), (2) adult and adult

Fig. 17.10. Locations of banded yearling males in relation to where they settled on territories as adults, Comox Burn$_{cp}$. Lines connect all sightings of an individual yearling to where he settled as an adult. Stippled areas include all adult hooting locations of that individual.



nests was 168 m (9–447 m, $n = 19$), and (3) first and second nests within years (renests) was 160 m (49–537 m, $n = 10$). None of these sets of data differs from another [12]. Only one nest site change exceeded 600 m, that of 1945 m, an extreme outlier at Hardwicke Island. Approximately two-thirds of all nests of individual females were <200 m from another of their nests, 90% were <400 m apart, and 98% were <600 m apart (Fig. 17.11). All are likely within the area of familiarity a female acquired in her first breeding season. A report that females have low fidelity to "summer range" (Bauer 1962) may reflect methods[24] rather than weak site fidelity. The bulk of evidence indicates that males and females, once committed, show equally strong fidelity to breeding areas.

17.2.3 Winter dispersal and site fidelity

Changes in winter home ranges between or among years might also be considered a form of dispersal, but there are few data on this subject. Three recent radio-telemetry studies, however, provide some information:

Middle Park: Among 10 grouse monitored in more than one winter, five adult males and five adult females, all were found in winter two <0.4 km from where they spent their previous winter (Cade and Hoffman 1993). Winter sites of four banded adult females (not radioed) were <0.3 km apart in consecutive winters, and two others were 0.1 and 0.9 km from where they spent their first winters, as juveniles.

Hardwicke Island: Among seven adult and yearling grouse observed in consecutive winters, all were within 200 m of their previous winter sites (Hines 1986*a*). Among 13 juveniles monitored on winter range, 10 returned to the same sites as yearlings. The others moved ≥1.5 km from first-winter sites to breeding range and became "essentially non-migratory" (p. 18). These data, too, suggest strong fidelity to winter home ranges, especially among yearlings and adults.

Miller Ridge: Pelren (1997) monitored three birds in consecutive winters, an adult male, an adult female, and a juvenile (winter one) male. All returned in winter two to within 200 m of sites occupied the previous year.

Combined data from these studies indicate all birds monitored in consecutive winters as yearlings and adults ($n = 23$) returned to, or very near to, winter sites occupied as yearlings. Among 16 first monitored as juveniles, 13 showed similar fidelity to winter home ranges and 3 changed sites (>1 km) between winters one and two. Although data are limited, they suggest strong fidelity to winter home ranges. That some juveniles changed winter sites in their second year (19% in this sample) may reflect that they were still involved in natal dispersal in winter one, with breeding home ranges not yet established. Perhaps location of first breeding site can influence that of second-winter site. We conclude, blue grouse exhibit strong fidelity to winter home ranges, with principal exceptions confined to some juveniles and likely influenced by natal dispersal.

17.3 Home range

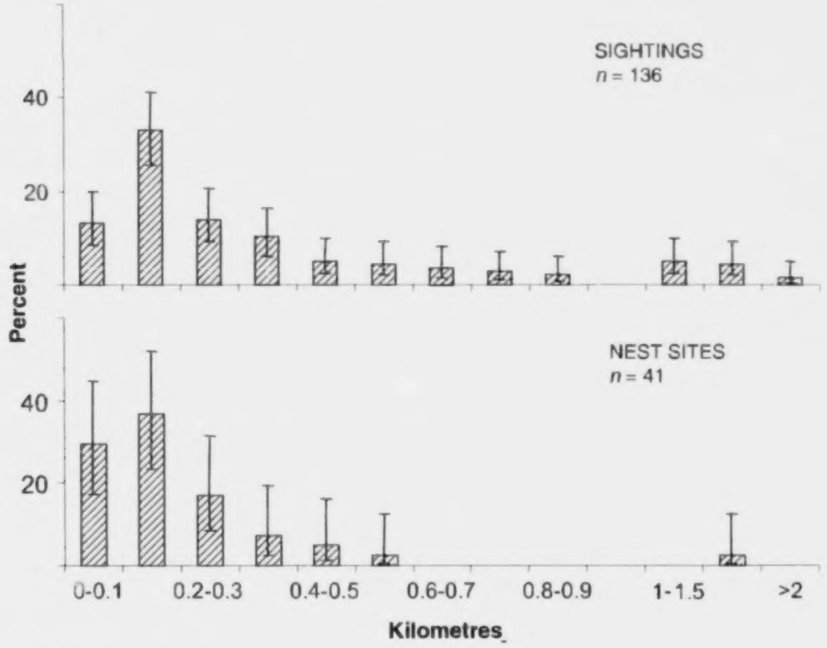
> *Notwithstanding their freedom of movement individual animals do not as a rule wander about at random, . . . the great majority spend their lives within closely limited areas.*
>
> LR Dice (1952)

The area over which an individual travels during its usual activities may be called its home range (paraphrased from Dice 1952); its usual area of use.[25] Size and shape of home ranges can vary with sex, age, intra- and inter-specific interactions, season, food, and cover, among others. Within these areas, activities may be concentrated in "centres of activity" (Smith 1974). Space included in a territory, in some cases a centre of activity, may or may not encompass an individual's entire daily or seasonal area of use. Home ranges have important potential implications to our understanding of social relationships, habitat selection, and demography. As migrants, blue grouse usually have separate breeding season and winter home ranges.

17.3.1 Males

There are two distinct classes of males on breeding range, those with territories, mainly adults, and those without, mainly yearlings. Home ranges of the two differ markedly, principally a reflection of territorial status, so we consider males by age class.

Fig. 17.11. Distribution of distances (km) between year-to-year geographic centres of April–May sightings of banded females, and between sequential nests of banded females (by %). Data for Comox Burn$_{\mathrm{cp}}$, 1962–1977, and Hardwicke Island, 1979–1984, combined.



(a) *Yearlings*. Yearling males arrive on breeding range after adults and at about the same time as adult females (see 17.1.3). Non-territorial yearlings tend to be secretive and hard to identify as individuals from bands alone, making determination of their home ranges difficult. Most data on home ranges of yearling males come from two studies with radio-marked birds (Sopuck 1979 and Jamieson 1983*a*).

Sopuck monitored 30 yearling males[26] at Comox Burn in the springs and summers of 1976 and 1977. Sizes of home ranges changed seasonally (Table 17.5), being larger from mid April to mid May than from mid May to mid June [13]. Longer movements early in the season may reflect the spring phase of natal dispersal. Among 28 birds that eventually localized, 68% had done so by 10 May, 86% by 20 May, and all by 30 May.[27]

The second telemetry study of yearling males was at Hardwicke Island. Jamieson monitored their movements from the third week in April to the third week in June in 1980 (*n* = 10) and 1981 (*n* = 14). He, too, reported a downward trend in size of home range from early to late spring and continuing into late summer. An all-season median size of 10.8 ha (Table 17.5) was similar to the mean reported for mid May to mid June at Comox Burn. Jamieson's Fig. 1 indicates that home ranges at Hardwicke Island were smaller than at Comox Burn in early and late spring; with medians of ~5 and ~3.5 ha in the two seasons, respectively. Population density was higher at Hardwicke than at Comox Burn and may explain this difference between areas.

Table 17.5. Size of breeding season home ranges of radio-marked yearling males at Comox Burn and Hardwicke Island.

	n	Mean (ha ± SE)	Range (ha)	Source
COMOX BURN				
16 April–15 May	17	26.8±4.9[a]	5.0–80.0	Sopuck 1979
16 May–15 June	22	11.9±1.4	4.3–24.1	Sopuck 1979
HARDWICKE ISLAND	?	10.8[b]	0.6–40.7	Jamieson 1982

[a] Correct mean is 26.8 ha rather than 28.5 ha as in Sopuck (1979).
[b] Median.

Two yearlings with adjacent home ranges at Comox Burn showed little overlap in their "core areas" of use from April to June (Sopuck 1979). Among four others, there was little overlap of core areas among three, with moderate overlap between the fourth and one of the others (our interpretation from Sopuck's Appendix 3). In the latter instance, Sopuck located both birds on the same day and at about the same time of day on 23 occasions, and only four times were they <100 m apart, only once <50 m apart. He suggested these birds were separated temporally.

At Hardwicke Island, home ranges of six radio-marked yearling males "overlapped to a high degree" (Jamieson 1982, p. 10). Analyses included home ranges throughout spring and summer, however, and which were changing as summer advanced. By late summer some males appeared to be "more aggregated" (Jamieson 1982, p. 29), which would tend to increase overlap.

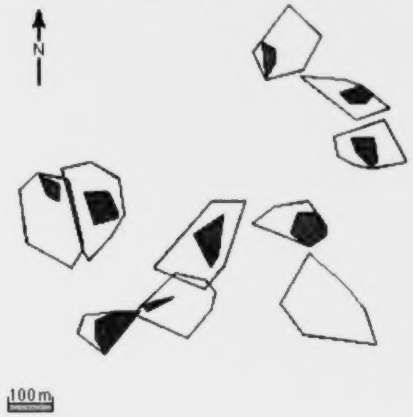
(b) *Adults*. Most adult males occupy breeding territories in spring and early to midsummer and on which they spend virtually all their time. Territories therefore equate to home ranges of these birds at these times and tend to be stable among years (see 17.2.2).

Size of spring–summer home ranges of adult males are much smaller than those of yearlings, ranging, on average, from 0.6 to 2.1 ha (Table 17.6). At Hardwicke Island, size changed seasonally, with a relatively restricted area of use up to mid May and a larger area of use after peak breeding (Lewis 1985*b*).[28] Most sightings in the period of peak breeding (68%) were within "activity centres", areas within which males hooted (Fig. 17.12). Lewis considered the total area used up to at least mid June[29] as territory, for he found little spatial overlap among adjacent males, as indicated by studies at Lower and Middle Quinsam (Bendell and Elliott 1967) and Comox Burn (McNicholl 1978).

Males tend to frequent particular hooting sites but may sing from other positions (see 16.3.2). Even when not singing, they are most often near these sites; within 15 m more than 80% of the time (McNicholl 1978). They are often in what appear to be "hideouts" (under, or adjacent to, logs, shrubs, or small trees). Most sightings away from these sites involve birds feeding or resting, or are by observers searching with dogs, which may have displaced birds before they were seen by the observer. Concentration of activities near favoured songposts during peak breeding likely explains the small home ranges at this time. Increased size of home ranges after peak breeding may reflect wider movements in search of food or other resources as breeding behaviour wanes. Data from radio-equipped males (Lewis 1985*b*) suggest many of the earlier reports of territory size of adult males (Table 17.6), based mainly on locations of hooting males, reflect activity centres rather than entire spring–summer home ranges.

In the very dense population at Lower Quinsam, ~80% of 215 consecutive sightings of individual territorial males were <60 m apart. In the sparse population at Middle Quinsam, among 61 consecutive sightings, <40% were <60 m apart (Bendell and Elliott 1967). These data agree with reported differences in size of territories at the two areas (Table 17.6) and led Bendell and Elliott to conclude that size varies inversely with density. This relationship reflects data from Vancouver and Hardwicke islands [14a], but does not do so across all populations (Fig. 17.13) [14b]. Mean territory sizes ranged from only 0.6 to 2.1 ha over a wide range in population densities, and reported maximums exceeded 2.8 ha in only one case. Perhaps a male cannot effectively defend >2–3 ha.

Fig. 17.12. Spatial relationships of territories of 10 radio-marked males at Hardwicke Island in 1981. Areas occupied until territories were abandoned are enclosed by outer lines; areas within which males hooted (activity centres) are shaded. There were four other territorial males in this area but with too few identifications to plot territories. Adapted from Fig. 1, Paper 2, of Lewis (1984*a*).



Some adult males do not acquire territories (Lewis and Zwickel 1980; Jamieson and Zwickel 1983*b*; Lewis 1984*b*; and 17.2.2(b)). These birds tend to be secretive and are rarely identified as individuals, making determinations of home-range boundaries difficult. Our impression from a few individuals for which some identifications were made is that they move over relatively wide areas that encompass territories of several adults. Their behaviour and size of home ranges appear

Table 17.6. Reported size[a] of breeding season home ranges of adult males in various regions.

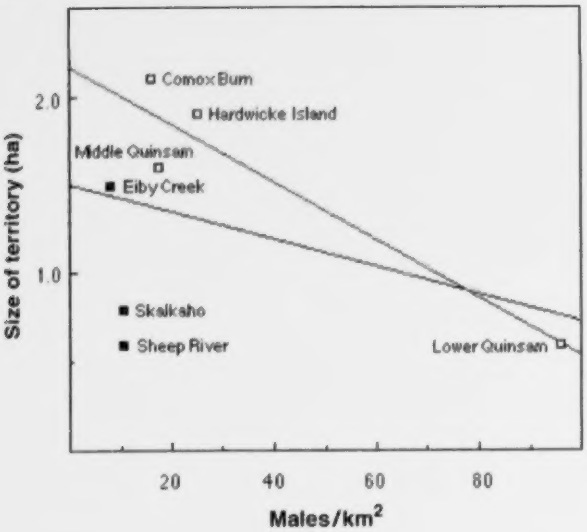
Area	*n*	Mean (ha ± SE)	Range (ha)	Source
Sheep River	11	0.6	0.2–0.9	Boag 1966
Skalkaho	27	0.8±0.04	0.5–1.5	Martinka 1970
Eiby Creek and Green Mt.	16	1.5	1.2–1.9	Hoffman 1981
Centennial Ridge	21?	0.7	0.4–1.1	Harju 1974
Lower Quinsam[b]	9	0.6	0.4–1.5	Bendell and Elliott 1967
Middle Quinsam[b]	11	1.6	1.3–2.8	Bendell and Elliott 1967
Comox Burn	32	2.1±0.3	0.4–5.2	McNicholl 1978
Hardwicke Island				
Peak breeding	10[c]	0.6±0.1	0.3–0.9	Lewis 1985*b*
All season	8[c]	1.9±0.2	0.9–2.8	Lewis 1985*b*

[a] Data are presented as territory sizes by most authors and in some cases are likely minimal because of limited numbers of identifications of some males (Bendell and Elliott 1967). They are, nevertheless, quite consistent within a narrow range across a wide spectrum of populations.

[b] Mean and range estimated by eye from Fig. 11 in Bendell and Elliott. One outlier of 4.5 ha at Middle Quinsam and considered aberrant by those authors is not included in range. Sample size from Bendell (1954).

[c] Birds equipped with radio transmitters.

Fig. 17.13. Mean size of territories of adult males regressed on density of adult males (birds/km^2) for Lower Quinsam, Middle Quinsam, Comox Burn$_{cp}$, Skalkaho, Eiby Creek, and Sheep River. Upper regression line is for Vancouver and Hardwicke island study areas only, the lower line for all areas.



similar to those of yearling males (Fig. 17.10) rather than of territorial adults (Fig. 17.8).

Bendell (1954) was first to examine spatial relationships of territorial males in any detail. His data, based on resightings of banded birds, indicated little overlap of areas used among adjacent males at Lower Quinsam between April and August. Even in that dense population, most territories were exclusive of those of others. Although no data on degree of overlap were presented it is clear from Bendell's Figs. 6 and 7 that it was small. Others have also reported little, or no, overlap of territories of adjacent males: Elliott (1967) at Middle Quinsam; Harju (1974) in southeast Wyoming; McNicholl (1978) at Comox Burn; Boag (1966) at Sheep River, but none provided data on amount of overlap.

Lewis (1985*b*) provided a quantitative measure of territorial overlap. Among 10 radio-marked males at Hardwicke Island there were three cases, with amount equal to 7% of the total area occupied by the 10 birds. There was no overlap among activity centres, suggesting most intrusions by territorial males into territories of others occur after peak breeding.

Several authors have examined dispersion of territories:[30] Bendell and Elliott (1967), at Lower and Middle Quinsam; Martinka (1972), at Skalkaho; and Lewis and Zwickel (1981), at Comox Burn. All reported uniform spacing, as determined by the Clark and Evans (1954) "nearest neighbor" test. At Lower and Middle Quinsam this was true for males in "very open" and "open" vegetation (preferred habitats) but not for those in "dense" and "very dense" habitats, where distributions did not differ from random. Bendell and Elliott suggested the lack of significance in the latter habitats may have resulted from small samples or an effect of openings in the vegetation.

In contrast to the above, Lewis (1985*a*) found a tendency (not significant) toward clumping of territories at Frazer Creek. He thought this was likely related to an association of territories with aspen thickets. We found a random dispersion of territories on our Skalkaho study area as a whole in 1986 [15a]. This area was composed of a mosaic of four principal plant communities (Fig. 16.2), and males were found almost solely in the two dominated by conifers. Within these, territories were spaced uniformly [15b], suggesting random spacing over the entire area was related to habitat selection among the mosaic of communities found there.

Table 17.7. Pre-incubation size of home ranges of radio-equipped yearling and adult females on breeding range at Comox Burn and Hardwicke Island.

Area, age, stage of reproduction	*n*	Mean (ha ± SE)	Source
COMOX BURN			
Yearling, pre-laying	12	20.7±5.1	Hannon et al. 1982
Adult, pre-laying	8	6.4±2.2	Hannon et al. 1982
Yearling, laying[a]	12	2.3±0.3	Hannon et al. 1982
Adult, laying	8	2.3±0.5	Hannon et al. 1982
HARDWICKE ISLAND			
Yearling, pre-laying	17	13.6±2.4	Hines 1986*a*
Adult, pre-laying	4	7.4±1.6	Hines 1986*a*
Yearling, laying	13	2.7±0.4	Hines 1986*a*
Adult, laying	7	2.8±0.5	Hines 1986*a*

[a] After localization near nest; the laying period.

17.3.2 Females

Except in early spring, home ranges of females differ more between stages of reproduction—pre-breeding, nesting, and post-hatch—than between age classes of birds. We consider females, yearlings and adults combined, as alone without nests (lone females), as those incubating nests, and as those with broods. Age class is considered, if relevant.

(a) *Lone females, except nest hens*. Adult females arrive on breeding range before yearling females, tend to return to the same areas used in previous years (see 17.2.2(d)), and, at Comox Burn, ranged over areas of ~6 ha prior to "localization" (Table 17.7). Yearling females moved over areas of ~20 ha prior to localization, presumably in search of a place to settle. Yearlings first ranged over larger areas than adults (Fig. 17.14), this being for them, the termination of natal dispersal. At ~10–15 days before laying, individuals in both groups localized on ~2–3 ha within the general vicinities where they nested (17.2.2(d)). Lance (1967) suggested localization coincides with "estrus". Data from radioed females at Hardwicke Island (Table 17.7) are in general agreement with those from Comox Burn.

Failed, or non-breeding, radio-marked hens[31] at Comox Burn used areas of ~5–6 ha, on average, in each 2-week period following loss of nest or chicks (Table 17.8). Among failed breeders, cumulative area used increased up to ~20 ha by 8 weeks after loss of nest or brood. Thus, these birds used relatively small areas within each 2-week period but expanded their total summer ranges as the season progressed.

Fig. 17.14. Pre-nesting movements of a radio-marked adult female and a radio-marked yearling female at Comox Burn. Adapted from Hannon (1978).

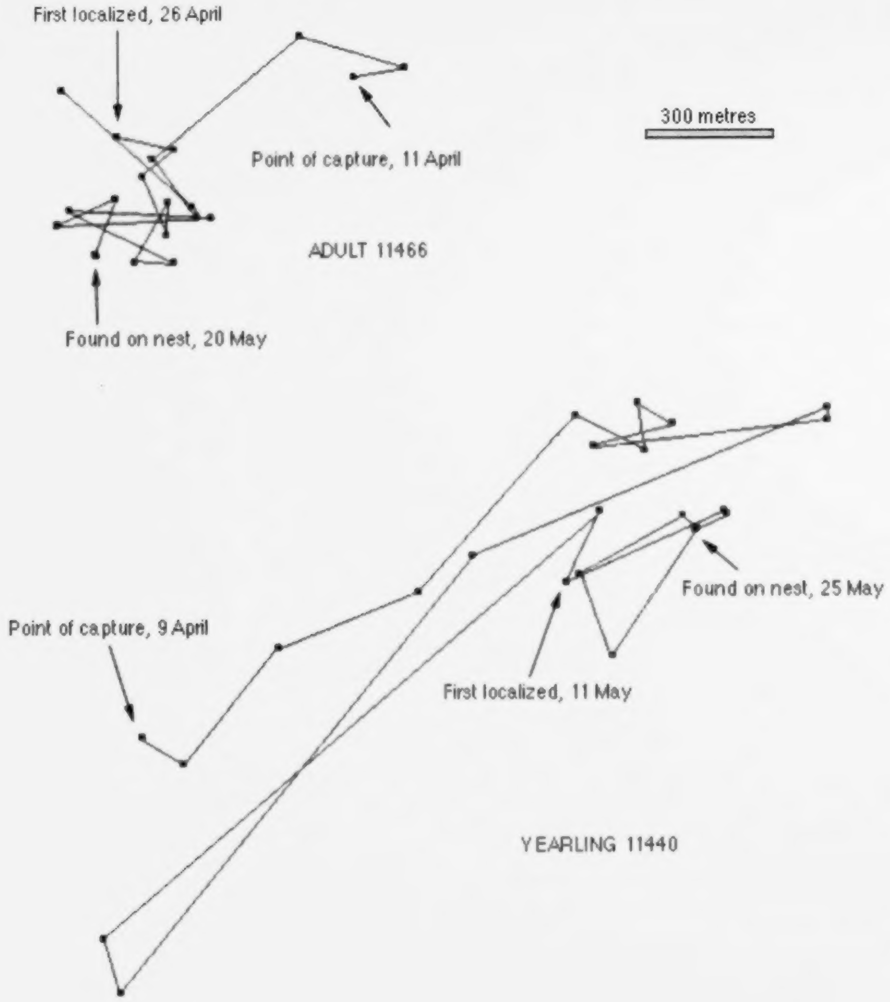

First localized, 26 April
Point of capture, 11 April
300 metres
ADULT 11466
Found on nest, 20 May
Found on nest, 25 May
Point of capture, 9 April
First localized, 11 May
YEARLING 11440

Table 17.8. Size of post-nesting home ranges of radio-marked broodless females at Comox Burn and in western Montana.

Area, time	n_{birds}	Hectares ± SE (range)	Source
COMOX BURN			
Bimonthly mean	22[a]	~5–6 (1.5–16.3)	Sopuck and Zwickel 1992
To 8 weeks after brood loss[b]	4	19.9±8.4 (5.0–43.5)	Sopuck and Zwickel 1992
MONTANA (western)	4	36.5±7.7 (18.0–51.0)	Schladweiler[c]

[a] Bimonthly sample sizes: 22 birds at 1–2 weeks, 18 at 3–4 weeks, 8 at 5–6 weeks, 4 at 7–8 weeks.

[b] Cumulative to 8 weeks after loss of nest or chicks.

[c] Personal communication.

Evidence is strong for little overlap in breeding season home ranges of territorial males, but females are a different story. Boag (1966, p. 804) reported an all-season mean home range size of 17.5 ± 3.2 ha (1.8–49.2 ha) for 15 adult females at Sheep River; home ranges "freely overlapped" one another. Bendell and Elliott (1967, p. 67) found that ranges of seven females at Lower Quinsam "completely overlapped", but they presented no examples and did not specify time period(s). We now know home ranges change temporally, i.e., prior to localization in spring, during localization, and post-hatch. We examine potential overlap for these periods.[32]

Hines (1986*a*) presented data on range overlap of females in spring. Among 11 adults at Hardwicke Island, 50% of their home ranges, on average, was shared with other adults, 73% with yearlings, and 84% with adults and yearlings. Among 14 yearling females, 46% was shared with adults, 82% with other yearlings, and 89% with adults and yearlings. After 1 May, the approximate time when adults localized, the picture changed sharply according to Hines's Fig. 8.5.[33] Ranges of 11 adults were shown, 3 of which appear to consist of only two locations, making an evaluation of their ranges difficult.[34] Among the others, ranges of four were separate from any other adult, and birds in two separate pairs showed slight to moderate overlap with each other. We calculated from these birds that only 8% of their total range was shared by more than one adult. Once localized, areas used appeared to be exclusive, or nearly exclusive, of those of other adults. We calculated median size of ranges of these eight females as 1.1 ha (mean = 1.4 ha, 0.7–4.2 ha).

Hines also depicted nine ranges of yearling females (on or after 1 May) in his Fig. 8.5, and only one pair showed more than minor overlap between any two yearlings, but considerable overlap with adults. Yearlings were clearly not yet localized, as median range size was 4.7 ha (mean = 4.8 ha, 1.1–9.5 ha, calculated by us). According to Hines, localized ranges of yearlings and adults did not differ (Table 17.7), and since yearlings localized ~10 days later than adults (Hines 1986*a*), a more instructive illustration would have compared ranges ≤10 days before laying for each age class rather than both from 1 May. We think some, if not most, indicated overlaps would have disappeared.[35] If so, here is evidence that breeding female blue grouse may have more or less exclusive home ranges in the late pre-nesting and nesting periods—perhaps territories, as suggested by Bergerud and Butler (1985), and as reported for female spruce grouse (Herzog and Boag 1978), capercaillie (Wegge 1984), and perhaps black grouse (Angelstam et al. 1985).

In May, at Lower Quinsam, "... two, three, and at times as many as six hens foraged within 50 feet [15 m] of each other in small clearings" (Bendell and Elliott 1967, p. 49). This suggests shared ranges by these hens. One cannot be sure whether all, or any, of these birds were localized for nesting, however, without knowing dates of the observations and ages of the birds involved. As well, birds may have come from different directions to favoured feeding areas at the edges of localized home ranges. These observations do not negate the possibility of more or less exclusive late pre-nesting and nesting home ranges.

In late spring and early summer, broodless hens include those still with nests, those that have lost clutches of eggs or broods through predation or desertion, or those that have not bred. Following completion of hatch, broodless hens include only failed breeders, or non-breeders. There are too few data on home ranges of broodless hens in summer to examine possible overlaps among them, or with other classes of birds.

After completion of hatch, the dispersion of lone females on an area heavily grazed by cattle on a shrub-steppe range, Balky Hill, was clearly different from that on nearby and ungrazed Frazer Creek (Zwickel 1973). In June, lone females were mostly in, or associated with, trembling aspen thickets at Balky Hill but dispersed throughout grasslands at Frazer Creek. By July and into early August, most lone hens were in, or associated with, thickets at both areas. These data suggest heavy grazing of the grasslands had an effect on the dispersion of lone females in early, and perhaps, late summer, a habitat effect.

(b) *Nest hens.* Home ranges of incubating females are small and, except the nest site itself, used mainly during brief periods off the nest (recesses) for feeding or other maintenance activities. T Mussehl and P Schladweiler monitored two radio-marked hens in western Montana that each confined their activities to <4 ha, beginning ~1 week prior to, and throughout, incubation (P Schladweiler, pers. comm.). These were generally similar to sizes of localized pre-nesting home ranges of females at Comox Burn and Hardwicke Island. One hen incubated for only 10 days, at which time her nest was destroyed. In the next 12 days she used an area of ~47 ha, after which she was not seen.

Lance (1967) provided data on distances from nests to feeding sites of two radio-marked incubating yearling hens at Comox Burn. One fed at three sites: 43, 79, and 94 m (mean = 72 m, $n = 7$ observations), respectively, from her nest.[36] The other fed at 10 sites, ranging from 14 to 75 m from her nest (mean = 36 m; $n = 17$ observations), significantly different from that of the first hen [16]. Areas enclosed in polygons connecting the outer points of feeding sites and nests of these hens were 0.37 ha and 0.35 ha, respectively. All feeding sites of the first female were "dry" (little succulent vegetation), but 6 of 10 of the second female were more "mesic". Seventy-five percent of her feeding trips were to mesic parts of the area. Most feeding sites of the second hen were not included within her subsequent brood range. Too few data are available to examine possible overlaps in ranges of nest hens.

(c) *Brood hens and chicks.* Radio-marked brood hens at Comox Burn used areas of ~5–6 ha, on average, during each 2-week period following hatch (Table 17.9). Cumulative area used increased up to ~20 ha by 8 weeks after hatch. These birds thus used relatively small areas within each 2-week period but expanded their total ranges as summer progressed, as with lone hens.

There is considerable variation in size of brood ranges among and within areas (Table 17.9). Bendell and Elliott (1967) noted that some broods range widely, while others remain within a relatively small area, as also indicated by other studies. More recent work with radio-marked birds indicates part of this variation may relate to age of hens, yearling or adult. Seven yearlings with chicks at Middle Quinsam moved farther from their nest sites in the first week after hatch, on average, than 14 adults[38] (Armleder 1980). So too did 7 of 16 radio-marked yearlings at Comox Burn (Sopuck and Zwickel 1992). There, two yearlings nested in dense forest and immediately after hatch moved >1 km to more open brood ranges (young seres). Sopuck and Zwickel concluded (p. 47), "... among hens that travelled extensively, adults remained near their nests while yearlings moved away". Some variations may be a result of differences between yearling and adult brood hens.

Recaptures of banded juveniles at Frazer Creek (Fig. 17.15) suggest short movements by broods while on summer range (median = 0.26 km). Twenty-eight percent were recaptured at the same site, and 80% ≤0.5 km, from where first caught (time between captures ranged from 0 to 36 days).

Table 17.9. Reported home range sizes of females with broods in various regions.

Area, time	*n*	Hectares ± SE (range)	Source
COMOX BURN			
Bimonthly mean	13[a,b]	~5–6 (1.0–15.0)	Sopuck and Zwickel 1992
Hatch to 8 weeks	3[a]	23.5±6.6 (13.8–36.1)	Sopuck and Zwickel 1992
MIDDLE QUINSAM			
Hatch to 6 weeks	18[a]	12.9±2.3 (3.2–39.2)	Armleder 1980
All season	13	12.2	Ash 1979
MONTANA (western)	15[a]	36.8±4.9 (16.0–77.0)	Schladweiler[c]
WYOMING (southeastern)			
3–6 weeks post-hatch	6	3.6±0.9 (1.6–7.6)	Harju 1974

[a] Birds equipped with radio transmitters.
[b] 13 birds at 1–2 weeks, 11 at 3–4 weeks, 8 at 5–6 weeks, 3 at 7–8 weeks.
[c] Personal communication.

Fig. 17.15. Distribution of distances (km) from sites of banding at which juveniles were recaptured within summers (by %), Frazer Creek, 1957–1961. Data extrapolated from Tables 10–12 of Henderson (1960) and Tables 24 and 25 of Bauer (1962).

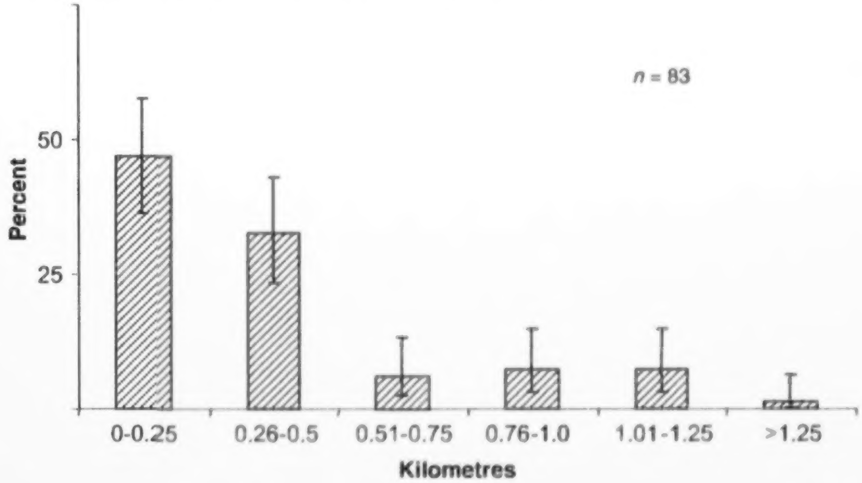


Table 17.10. Distances moved (m ± SE) by radio-marked brood hens from day to day on Vancouver Island and in western Montana.

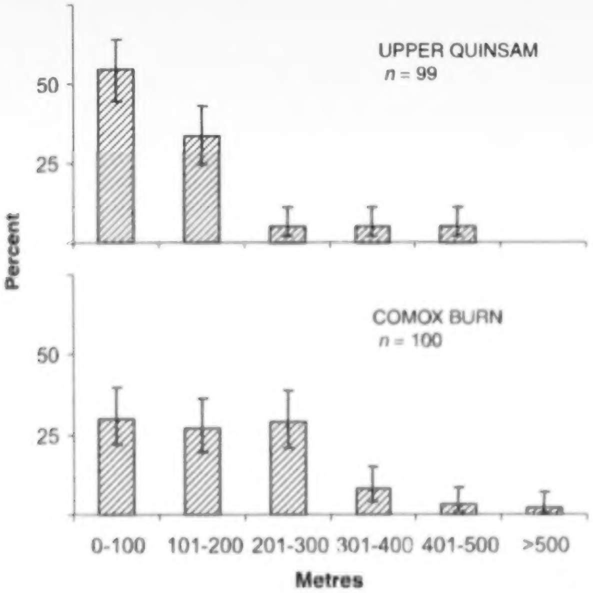
Area	n_{broods}	$n_{\text{observ.}}$	Mean distance	Source
VANCOUVER ISLAND				
Middle Quinsam	7	100	218±17	Armleder 1980
Comox Burn	8	100	190±23	Armleder 1980
Long Lake	4	100	151±15	Armleder 1980
Upper Quinsam	4	99	128±14	Armleder 1980
MONTANA (western)	13	227	236	Schladweiler[a]

[a] Personal communication, letter 13 March 1991.

Others also have reported relatively restricted moves by hens with broods, as based on consecutive sightings of banded birds: Bendell (1954), ≤800 m; Boag (1958), usually <800 m; Mussehl (1966), mean = 399 m, *n* = 6 broods; Harju (1974), up to 300 m; and Weber (1975), ≤550 m.

Day-to-day moves by broods are relatively short, averaging <250 m, as indicated by radio-marked brood hens at five sites (Table 17.10). Mean daily moves were significantly longer at Middle Quinsam and Comox Burn than at Long Lake and Upper Quinsam (subsidiary study areas to Middle Quinsam; Armleder 1980). Over 50% of those at Upper Quinsam were ≤100 m, and 87% ≤200 m. At Comox Burn daily moves were more evenly distributed among distance categories (Fig. 17.16). Even there, however, 86% were ≤300 m. Armleder found no differences by age of chicks from hatch to 6 weeks of age, between daily moves of yearling and adult brood

Fig. 17.16. Distribution of distances (m) moved each day (in %) by four brood hens at Upper Quinsam and eight at Comox Burn, by 100-m intervals. Data extrapolated from Fig. 8 of Armleder (1980).



females, or among populations of different densities. Differences among areas likely relate to local dispersion of resources.

Once hatch occurs, ranges of hens with chicks increase greatly (Table 17.9). At Middle Quinsam, "Different broods crossed and recrossed portions of the study areas, all appearing to share the summer range" (Bendell and Elliott 1967, p. 51). The implication is that brood ranges overlapped greatly. At Upper Quinsam and Long Lake Armleder (1980) examined the dispersion of radio-marked brood hens. Only 7% of the total area used was shared by two or more broods. He concluded (p. 30), ". . . brood hens moved about on almost exclusive areas". Perhaps Armleder had too few hens marked to obtain a complete picture of brood range dispersion?, for in western Montana, Mussehl and Schladweiler (1969) show extensive overlap in the ranges of seven radio-marked brood hens, more in line with the suggestion of Bendell and Elliott (1967).

Broods are sometimes found together (Caswell 1954*b*; Elliott 1965; pers. observ.), but are most often alone, at least in early summer (Bendell and Elliott 1967; Zwickel 1973). In a 2-year sample at Comox Burn, among 154 brood sightings (13% in June, 49% in July, 38% in August), not one was ≤10 m from another (Zwickel 1992). On the shrub-steppe Frazer Creek and Balky Hill study areas, broods were widely dispersed over grasslands on both heavily grazed and ungrazed areas in June, when chicks were small, but more often in or near thickets in July and August (Zwickel 1973). This contrasts with lone females in June (see above), which were mainly in or near thickets on the heavily grazed area but widely dispersed on the ungrazed area. Both groups were more often in or near thickets at both areas in July and August. Thus, although lone hens seemed to react to heavy grazing of grasslands by associating with thickets, those with young chicks remained dispersed. This may reflect an avoidance of one another by hens with young chicks, an avoidance that may end as chicks become older and maternal behaviour wanes.

In shrub-steppe habitats, where grasses and forbs, especially, desiccate badly, some broods may aggregate in mid to late summer (Weber 1975), tending, at Frazer Creek, to move from higher ridges into aspen thickets in the bottoms of draws or gullies. Hens with chicks often gravitate toward mesic sites (Wing et al. 1944; Mussehl 1963*a*; Bendell and Elliott 1967; Lance 1967; Donaldson and Bergerud 1974), presumably to feed and (or) for comfort. Thus, habitat selection may bring them together and contribute to range overlap. Early season exclusivity would then be temporal, with a more common use of space later in the season.

Aggregations in late summer, especially on interior ranges, may reflect the beginning of brood breakup, a subsequent mixing of broods (Wing et al. 1944; Weber 1975), and the initial stage of natal dispersal. This too contributes to reports of range overlap.

17.3.3 Winter

Winter is a period for which only limited amounts of home range data are available. Information comes almost exclusively from three studies with radio-marked birds: Cade (1985), Hines (1986*b*), and Pelren (1997). At Middle Park, winter home ranges of yearlings and adults (Table 17.11) were significantly smaller than those of juveniles (Cade 1985). One juvenile female ranged over 18.7 ha in her first winter but over only 3.5 ha the following year. Ranges of juveniles were similar in size to those at Hardwicke Island.

Winter ranges of adults at Miller Ridge were also significantly smaller than those of juveniles (Pelren 1997), but were considerably larger for both age classes than at Middle Park and for juveniles at Hardwicke Island.[38] One point seems clear, even from these limited samples—first-winter birds have larger home ranges, on average, than older birds. Young birds may still be attempting to establish themselves within the social system. Larger winter ranges at Miller Ridge than at Middle Park and Hardwicke Island might relate to a wider dispersion of suitable winter trees in the parkland community there.

Table 17.11. Winter home range sizes of blue grouse at Middle Park, Hardwicke Island, and Miller Ridge.

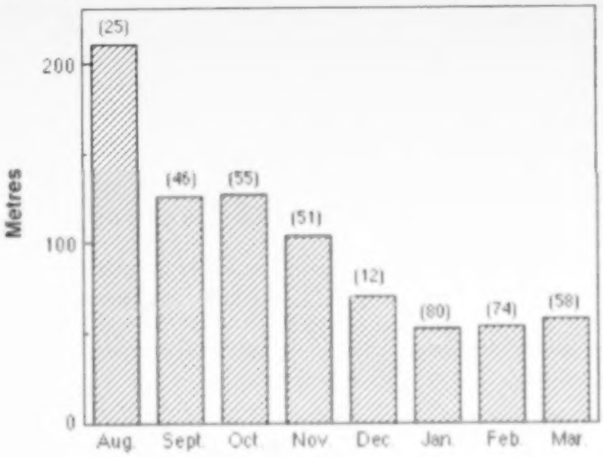
Age class, area	*n*	Mean (ha ± SE)	Range (ha)	Source
YEARLING/ADULT				
Middle Park[a]	10	3.0[b]	1.6–7.1	Cade 1985
Miller Ridge	19	28	2–90	Pelren 1996
JUVENILE				
Middle Park[a]	3	18.7[b]	9.2–42.2	Cade 1985
Hardwicke Island	21[c]	16.8±2.3	3.0–42.5	Hines 1986*b*
Miller Ridge	13	67	17–211	Pelren 1996

[a] Data from Green Mt. and Whiteley Peak combined.

[b] Median.

[c] Sample includes 20 juveniles and one adult female (not separated in manuscript by Hines).

Fig. 17.17. Median daily movements (m) of radio-marked juveniles at Hardwicke Island by month, August to March. Data extrapolated from Fig. 4.4 of Hines (1986*b*). Sample sizes are in parentheses.



At Middle Park, Cade (1985) maintained records of how many different stands of conifers were used within a winter by 13 individuals. Three adults used only one stand of trees; six adults and one juvenile, two stands; one adult and one juvenile, three stands; and one juvenile, four stands. Most (77%) were moving among or between different stands of trees, but one adult female was found six times in the same tree from January to March. Distances moved are almost certainly related in part to the local dispersion of suitable conifers within an area.

The only information on day-to-day movements in winter are from juveniles at Hardwicke Island (Hines 1986*b*). Here, median daily movements became progressively shorter from August to December (Fig. 17.17), after which they remained relatively stable through March, at ~50 m/day. Since winter home ranges of adults are much smaller than those of juveniles, we suspect their daily movements are even more restricted, a conclusion consistent with reports that blue grouse are very sedentary in winter (Munro 1919; King 1971; Cade 1985).

To the best of our knowledge, only Hines (1986*b*) has presented information on overlap of winter home ranges for blue grouse. His Fig. 6 shows extensive range overlaps among 16 radio-marked birds on a part of Hardwicke Island. Unmarked birds also were present, increasing the probability that overlaps were even greater. Winter flocking is common in blue grouse (see 15.4.1(a)), so substantial range overlap is to be expected.

17.4 Synthesis

Migration. Migration involves a seasonal change in home range, with most grouse wintering in medium to dense conifer forest and moving into more open forest or shrub-steppe communities in breeding season. Movements tend to have a strong vertical component, with birds in most populations moving up to winter and down to breed, opposite to that of most species in montane areas. Nevertheless, some populations or individuals show little seasonal movement, while others breed in subalpine areas and presumably move down into forest to winter. Differences likely reflect the proximity of breeding habitat to that used in winter.

In spring, movement from winter to breeding range is rapid, with clear differences among sex and age classes. Return to winter range is more protracted, extending over several months; again, with clear differences among sex and age classes. In both instances, movements of individuals likely involve only days. Some birds may establish summer home ranges after leaving breeding range, however, making final moves to winter range at a later date. Many of the differences between sex and age classes relate to reproductive events.

Some birds are essentially non-migratory, with others moving up to 35 km or more between breeding and winter ranges, at times passing through suitable habitat before arriving at their destinations. Birds in all populations studied move toward nearby upland conifer forests to winter, irrespective of compass orientation.

Most observations suggest blue grouse move singly or in small groups in both spring and post-breeding migration, but there are reports of flocks of up to 100 birds in transit. Most chicks appear to have separated from their mothers and siblings by the time they settle for winter. Their movements likely reflect a tendency to both migrate and disperse.

The ultimate stimulus for migration in blue grouse is likely an adaptation for breeding in relatively open habitat, coupled with an obligate, or near-obligate, dependence on conifer forest in winter. One outcome is that most blue grouse spend 6 months or more on winter range, length depending on sex, age, and for females, reproductive success. Although much evidence pertaining to migration comes from our studies in coastal British Columbia, most patterns there are consistent with those from other populations for which data are available.

Dispersal and site fidelity. Natal dispersal usually involves an autumn move to a winter site, but the stimulus that elicits settling for winter is unknown. It is likely related in part to social factors. We suspect spring moves are most important in determining locations of first breeding home ranges, hence natal dispersal distances. Documented natal dispersal distances tend to be much shorter than those for migration, none exceeding 12 km, but reported distances must be considered minimal.

Much evidence suggests yearling and adult males and yearling and adult females are strongly philopatric, returning to the same breeding and winter home ranges from year to year. Only between juvenile and yearling life stages are there significant shifts in home ranges between years.

Home range. As with many other species, size of home ranges of blue grouse varies seasonally. Spring ranges of adult males, most of which occupy territories, are relatively small and on which they spend virtually all their time. Most of their time in the peak mating period is spent in a relatively small centre of activity, and ranges expand following this period, but have little overlap with those of other adults. Yearling males and non-territorial adults range over relatively large areas that encompass home ranges of several territorial males in spring and summer. Some evidence indicates there is little overlap in core areas, or activity centres, among yearling males.

Home ranges of females change throughout spring and summer. On arrival on breeding range, yearlings move over larger areas than adults, likely reflecting the spring phase of natal dispersal. Females that breed greatly restrict their ranges in the general vicinity of where they will nest. Some evidence indicates that late pre-nesting and nesting ranges may be more or less exclusive, perhaps territories.

Following hatch, some hens, especially yearlings, establish brood ranges well away from where they nested, indicating that immediate access to requirements for chicks does not explain nest site selection. Brood ranges tend to be much larger than those of territorial males. Nevertheless, there is considerable variation in size, and this likely reflects local dispersion of resources. Broodless females are most often found alone, indicating mutual avoidance or exclusive use of space; we suspect the former. They appear to have summer ranges equivalent in size to those of brood hens.

These grouse, especially adults, tend to be sedentary in winter, living on smaller home ranges than in spring and summer. First-year birds have the largest winter ranges, likely a reflection of this being a part of natal dispersal. But even their movements are relatively small. Daily movements of first-year birds decreased from autumn to December at Hardwicke Island and were relatively stable from January through March. Perhaps these birds had established themselves within winter social systems by this time. There is substantial overlap in ranges of wintering birds, a reflection of a tendency for flocking at this season.

Information from Middle Park, where the forest is fragmented, indicates blue grouse may move among different stands of trees in winter. Degree of forest fragmentation may help explain much larger winter ranges reported for birds at Miller Ridge than at Middle Park and Hardwicke Island. How much fragmentation might be too much for acceptable winter range is unknown, but this could become a problem as logging encroaches on such areas.

Endnotes [Chapter 17]

1. Capercaillie also exhibit "reverse" migrations in some areas (Dorst 1962; Kuz'mina 1992).

2. Among the four sex and age classes, adult males are most easily identified in spring owing to display behaviour and accounting for the large sample of these birds in Fig. 17.1. Many females are not identified until with brood, on or after 15 June at Comox Burn. Yearling males are first identified at a fairly steady rate throughout their time on breeding range.

3. Wing et al. (1944) observed males and lone females moving up slope prior to such moves by hens and chicks. Caswell (1954*b*) and King (1971) interpreted disappearance of birds from particular areas and influxes into, or through, others as evidence of migration. On Vancouver Island, Hatter (1955) noted a <1% take of adult and yearling males by hunters, with the harvest comprised principally of females [and chicks]. He interpreted this as evidence that males were already (early September) on winter range at upper elevations and relatively invulnerable to hunting.

4. High numbers of contacts of males from March to June are partly a result of greater ease of finding singing males than females. An increase in numbers of brood females over summer is partly related to growth and conspicuousness of broods.

5. The latter may have settled on summer range and later moved to winter sites.

6. No females were monitored beyond 9 October, so further movements may have occurred before settling for winter.

7. Recoveries by hunters reflect areas hunted and may not be representative of all birds (Bendell and Elliott 1967), especially since blue grouse often are moving from relatively accessible breeding areas toward less accessible winter habitats. Since many birds likely had not reached winter home ranges, distances are almost certainly minimal.

8. Hunting recoveries include many juveniles whose movements may represent the fall phase of natal dispersal rather than migration (Zwickel 1992). Migratory patterns for these birds will not be established until they have established first-winter and subsequent breeding home ranges.

9. Lack of recoveries west of Mt. Washington and toward Mt. Brooks reflects that much of that area is in Strathcona Provincial Park and closed to hunting.

10. Marked grouse identified at Middle Park in winter included 4 adult males, 2 juvenile males, 14 adult females, and 6 juvenile females.

11. Data here are partly confounded because many juveniles disappeared, with fates unknown. If more than seven left the island, distances reported were minimal.

12. Easterly moves up to ~10 km and westerly moves up to 6–7 km were possible while remaining on the island; westerly moves would tend to take birds to lower elevations and into mainly old second-growth forest. Birds could not travel more than ~2–3 km to the north or south without crossing large expanses of open water.

13. Males in most populations also shift heavily, exclusively in some shrub-steppe populations, to non-coniferous foods in spring and early summer. Where territorial males are mainly arboreal, however, they may feed heavily on conifers throughout the year, supporting the suggestion hens and chicks are most important in this scenario.

14. A caveat must be noted. If individuals are marked mainly on limited study areas and monitoring is most intense on those areas, individuals that settle outside the boundaries are less likely to be found. Size and shape of study area also affects rates of later detection. Recent advances in radio-telemetry reduce these problems but do not eliminate them. All studies of dispersal in blue grouse suffer from these problems, so reported dispersal distances should be considered minimal.

15. Our two main study areas at Comox Burn, the control plot, Comox Burn$_{cp}$, and Tsolum Main, were monitored intensively from 1969 to 1977, an area of 1110 ha, with an intermediate buffer area monitored all years, but less intensively, a total area of 1764 ha. In addition, ~700 ha surrounding Tsolum Main was searched periodically in mid to late summer of most years, making the entire area monitored >24 km^2. Maximum length of the three main areas combined was 7.9 km, average width, ~2.5 km (~1.5–3.2 km).

16. Criteria for determining natal dispersal distances were slightly different than those of Jamieson and Zwickel (1983). We used location where wing-tagged or banded as an approximation of a bird's natal home range. In subsequent years, first sighting of the year was used to approximate a female's home range, for in most cases that would most closely approximate the nest site. First sighting was used for yearling males and adult males not seen hooting, but, if available, first sighting when hooting was used. No sightings were used after 30 June because of the probability birds might have abandoned breeding home ranges by that time. If an individual was seen in more than one year, an average of annual first sightings was used to estimate that bird's breeding home range.

17. Yearling males are a special case, for most do not hold territories and presumably do not breed. Since they can, however, we consider changes between home ranges as yearlings and those occupied as adults as breeding dispersal.

18. Annual boundaries reflect locations where birds were specifically identified each year, not necessarily total areas used.

19. Non-territorial adults are more secretive than those with territory.

20. Movements <1 km from site of capture.

21. One bird left Comox Burn and was found 8 km away (Sopuck 1979), but the date found is not reported, and this may have been a migratory movement; it was not included in Sopuck's home range calculations.

22. All birds with two or more identifications as yearlings between 1972 and 1975, plus four identified only once are included in Fig. 17.10. Straight-line distances to the nearest boundary sighting as an adult are shown. Territorial adult locations include all identifications for each individual between 1973 and 1977.

23. Within years, the geographic centre of April–May locations was used to estimate breeding site for each female, but if a nest site was available, that was used.

24. Most birds banded by Bauer and associates were marked only with numbered aluminum bands, and had to be recaptured for subsequent identification.

25. An individual may make occasional "excursions" outside its normal home range, e.g., if chased by a predator or in pursuit of a competitor or unusual breeding opportunity. See Glossary for a more specific definition of home range.

26. Movements of most were monitored from April or early May until departures toward winter range.

27. Percentages calculated by us from data in Sopuck's Fig. 12.

28. Lewis defined the breeding period as 8 April to 20 May and peak breeding as the modal 2 weeks of the breeding period.

29. Mid June is when some territorial males abandon territories, but a few may stay on them into August, rarely September.

30. Spacing among home ranges may have important implications to demography and interpretations of social behaviour. Three patterns of dispersion are usually recognized, random, uniform, and aggregated (Clark and Evans 1954). Here, we use spacing to refer to the dispersion of territories, ". . . the distribution or physical location of individuals [territories] within a population at a particular moment in time" (Emmel 1976, p. 161).

31. Following incubation there are three classes of females on breeding range: non-breeders, unsuccessful breeders, and brood hens. Birds in the first two classes are not easily separable, and we combine them for analysis as lone, or broodless, hens.

32. Since females tend to be secretive prior to hatch, we examine this question mainly on the basis of studies with radio-marked birds.

33. If we interpret Hines correctly, home ranges in his Fig. 8.5 represent locations from 1 May to initiation of incubation.

34. Two were exclusive, or nearly exclusive, of any other adult, and one had a nearly complete overlap with another adult and partial overlap with a second.

35. This points out the importance of analyses being time specific, in this case relative to reproductive phenomena rather than calendar date.

36. Data extrapolated by us from Lance's Appendix 4, Fig. 14.

37. Armleder reported that hens in either age class might have brood ranges well away from nest sites, but did not mention whether yearlings or adults are more likely to do so.

38. Birds at Miller Ridge made extensive moves in early March, when still classified as on winter range. Breeding here is very early relative to the other areas (Fig. 10.3), and these birds may have been moving onto or toward breeding areas, thus accounting for the large winter home ranges reported.

Part 5

Population Parameters, Predators, and Disease

CHAPTER 18

Population Parameters

The basic characteristic of a population that we are interested in is its size or density. The primary population parameters that affect size are natality, mortality, immigration, and emigration.

Charles J Krebs (1972)

All populations fluctuate and densities differ among areas. The mechanisms and (or) factors that determine numbers on an area over time, or cause differences among areas, are major questions in population biology and a central problem in ecology. These questions, especially with respect to blue grouse, will provide the principal basis for a future publication. Here we document population parameters, e.g., densities, age structures, and survival rates reported for blue grouse in various parts of their range, leaving attempts to explain most changes and differences to the later work. See also 10.6 for parameters directly associated with reproduction.

18.1 Population density

18.1.1 On breeding range

Most blue grouse are migratory, and density on a particular area may vary widely in different seasons. Highest densities in most regions almost certainly occur when birds are concentrated on breeding range, for at other seasons individuals from a given population may be spread over large expanses of winter range (Bendell and Elliott 1967; Zwickel et al. 1968; Cade and Hoffman 1993). Even in breeding season, densities change because of the annual increment of young, ongoing mortality, and early return of many males and some non-breeders and unsuccessful breeders to winter range.

We use breeding density to refer to numbers of yearlings and adults that come onto, and settle on, an area in the period of peak breeding. This represents the maximum number of potential breeders, although most yearling males do not breed (Bendell and Elliott 1967), and some adult males (Lewis and Zwickel 1982) and yearling females (Hannon and Zwickel 1979; Zwickel 1980) may not breed.

(a) *Males*. Yearling males are difficult to census, and certain assumptions must be made to estimate their numbers—e.g., one can assume ~30% yearlings among all males, the approximate annual mortality rate of adult males in most populations, to estimate total numbers of males in stable populations (Zwickel and Bendell 1967*b*). Since most adults, and few yearlings, hold territory, numbers of territories give a close approximation of the number of adult males on breeding range.

Reported densities of territorial males vary widely (Table 18.1). Those at Lower Quinsam and Copper Canyon were 2–3 orders of magnitude higher than recorded for any other population. Extremely high densities reported for those areas may be somewhat inflated because of relatively small census plots,[1] with that at Copper Canyon further complicated because few males were marked. Nevertheless, data from hunting harvests (Redfield et al. 1970) indicate that density at Lower Quinsam and adjacent areas was extremely high from 1950 to 1952.

In general, densities in interior populations are lower and fluctuate less than those on some coastal clear-cuts (Table 18.1). An exception is the Sheep River population, which declined from 19 to 2 males/km^2 between 1955 and 1964 (Boag 1966).[2] Less stable, coastal populations likely reflect that most studies there were on areas in rapidly changing early forest seres. These are areas where blue grouse have reached highest densities. Unfortunately, few data are available for coastal birds outside British Columbia. The two subalpine populations studied to date, one interior and one coastal, were at low density when studied.

In spring 1976, Frandsen (1980) censused territorial males on 17 areas of Vancouver Island, all of which were in young forest seres, ranging from 7 to 25 years post-clear-cut logging. Size of areas varied from 340 to >9900 ha. His counts were done along road transects where males were induced to sing with tape-recorded playbacks of female calls (Stirling and Bendell 1966). He reported 2–33 males/km^2, well within the range of numbers for other populations in this region.[3] The lowest density reported for any population, 0.16 males/km^2, was on coastal clear-cuts in southeast Alaska (Doerr et al. 1982). Numbers in nearby old-growth forest at the same time averaged 7/km^2, a remarkable difference and opposite to what studies on Vancouver Island suggest, high in clear-cuts and low in old-growth.

Bland (1993, 1997) censused "hooting groups" of *D.o. sierrae* in selected areas in California in 1992. Groups ranged in size from 1 to 5 birds. On the basis of amount of area occupied by these individuals, he reported densities of 3–14 males/km^2 but did not provide estimates over larger areas. Many groups were apparently widely separated, and these figures are not comparable to those reported by most workers (Table 18.1).

Table 18.1. Reported densities of adult males (birds/km^2) on various breeding ranges.

Area	Years of data	Density	Source
INTERIOR SUBSPECIES			
Duck Creek (691)	1	2[a]	This study
Green Mt. (181)	6	9–10	Hoffman 1981
Eiby Creek (482)	5	6–7	Hoffman 1981
Skalkaho (477)	6	7–9[b]	Schladweiler 1968
Skalkaho (477)	2	8[b]	Martinka 1970
Skalkaho (505)	1	14	This study
Frazer Creek (256)	1	13[a,c]	Lewis 1985*b*
Sheep River (251)	10	2–19	Boag 1964
Hudson Bay Mt. (547)	1	3[d]	This study
COASTAL SUBSPECIES			
Lower Quinsam (110)	1	27[a]	Fowle 1960
Lower Quinsam (29)	3	90–103	Bendell 1955*c*
Middle Quinsam (100–323)	19	10–25	Zwickel et al. 1983
Comox Burn$_{cp}$ (485)	13	12–20	Zwickel et al. 1983
Comox Burn$_{cp}$ (485)	3	12	Mossop 1971
Mt. Washington (1112)	1	4[a,d]	King 1971
Copper Canyon (17)	2	86[a]	Mossop 1971
Ash River (117–445)	4	9–25[e]	Redfield 1975
Hardwicke Island (465)	5	17–33	Zwickel et al. 1988
Hardwicke Island (95)	3	18–29	Lewis 1984*a*
Prevost Island, BC (688)	2	6–10	Donaldson and Bergerud 1974
Southeast Alaska (290–605)	2	0.16–7	Doerr et al. 1984
May Ranch (696)	1	2[a]	This study

Note: Size (ha) of census plot(s) at each area is in parentheses; in some cases represents a total area for more than one plot.

[a] No birds marked.

[b] Calculated by us on the basis of a revised study area size of 477 ha.

[c] Calculated by us from Lewis's Fig. 1 and data in his text.

[d] Subalpine population.

[e] Extrapolated from graph (three study plots, with maximum densities on two > 15).

Table 18.2. Reported densities of adult plus yearling females (birds/km^2) on various breeding ranges.

Area	Years of data	Density	Source
INTERIOR SUBSPECIES			
Green Mt. (181)	6	9–12	Hoffman 1981
COASTAL SUBSPECIES			
Comox Burn$_{cp}$ (485)	10	21–29	This study
Ash River (117–445)	4	21–62[a]	Redfield 1975
Hardwicke Island (465)	6	26–83	Zwickel et al. 1988
Hardwicke Island (95)	2	53–62	Lewis 1984*b*

Note: Size (ha) of census plot(s) at each area is in parentheses.

[a] Extrapolated from graph (three study plots, with maximum densities on two > 32 birds).

(b) *Females*. Numbers of females are more difficult to determine, and few direct estimates have been attempted (Table 18.2);[4] most authors assume a balanced sex ratio in the breeding population and use numbers of territorial males, weighted to include non-breeding yearling males, as an index to numbers of females. The only independent data for an interior population, at Green Mt., suggested a relatively stable population at moderate density. As with males, recorded densities of coastal females were higher and fluctuated more widely than in the interior. Numbers at Hardwicke Island declined from very high (~83/km^2) to moderate (~26/km^2) density between 1979 and 1984. When at its peak, 1979, >75% of the females were individually marked, helping to confirm that densities approaching those reported at Lower Quinsam for males are possible.

(c) *Broadscale geographic differences*. In 1978 and 1979, we conducted an extensive survey of blue grouse in selected areas throughout their range (Bendell and Zwickel 1984). More than 40 areas were visited and rated for relative breeding densities. To the east and west, barriers to distribution (prairie to the east and the Pacific ocean to the west) were sharp and did not relate to density except as barriers to distribution, i.e., density dropped sharply to zero, but up to these points there was no east–west trend. In contrast, densities near the southern and northern extremes of distribution were low, with highest densities, in a latitudinal sense, more centrally located.

(d) *Fluctuations within seasons*. As the breeding season progresses, marked changes in density occur, and it is perhaps impossible to be precise about numbers of grouse on any extensive area at any point in time. When eggs hatch, young of the year are added to the population, and at about this time, many adult and yearling males and unsuccessful and non-breeding females begin their return to winter range (Sopuck 1979, 1985*b*). In coastal areas, especially, a few males may stay on territory into early September, but in at least lowland interior populations most are gone from breeding range by the end of June or mid July (see 17.1.4). Soon after hatch, some broods leave areas where born, others stay. And there is a steady attrition resulting from mortality, especially pronounced among very young juveniles (Zwickel and Bendell 1967*b*). Density on breeding range is in a constant state of change, beginning as early as mid May and extending into mid autumn.

Numbers may change very rapidly on breeding range. For example, between 15 and 29 July 1958, Henderson (1960) recorded 423 sightings of blue grouse in 71 h of search on the Frazer Creek study area, a mean of 6/h. One month later, between 14 and 21 August, he saw 87 grouse in 30 h, ~3/h. By late August, very few grouse were being seen, and on 30 August a 3-h intensive search of the entire plot by two persons and one dog netted one grouse. This was a warm summer and the vegetation was very dry, which likely caused a rapid movement, mainly hens with broods, off the area. In contrast, Bendell and Elliott (1967) suggested that few brood hens leave summer range before 1 September on Vancouver Island. Lance (1967), Sopuck (1979), and Hines (1986*a*) found on Vancouver and Hardwicke islands that of seven radio-marked brood hens, none left breeding range until at least 1 September, consistent with this suggestion. Sopuck noted that most radio-marked broodless hens had left 2–6 weeks earlier. These examples illustrate some of the problems in estimating densities beyond the hatching period.

18.1.2 Outside the breeding season

Most of the blue grouse year is spent off breeding range in most populations studied; up to perhaps 9 months each year by many males and some females. Birds from a local population may be spread over an area many times larger than the size of breeding range from which they came (17.1.4(c) and 17.1.4(d)). Here they likely share winter range with birds from other areas, but this is not well documented.

There are few studies on winter range, and only King (1971) has provided information on winter density. He found only males on his study area on Vancouver Island in winter,[5] an estimate of 15 on ~24 km^2, <1/km^2. This grouse is mostly arboreal at this time and difficult to census. King's estimate was almost certainly minimal.

Most intensive studies of blue grouse have been conducted in areas where there appears to be a vast amount of winter range relative to breeding range. Winter densities must be more sparse than on breeding areas in such areas. In other regions, however, winter range may be restricted. For example, in some disjunct populations in central Nevada, small, open stands of limber pine represent the only conifer present on wintering areas (Fig. 7.11), and numbers may be higher than on associated breeding ranges, but this is speculative. Winter densities are a major unknown, and suitable winter range might limit breeding density in some populations.

18.2 Sex ratios

The number of males:females may have important implications to kinds of mating systems and dynamics of populations. Although balanced at birth in most birds, sex ratios may change with age or vary among populations of the same species because of differential mortality within the sexes (Emmel 1976). As well, observed ratios may differ from actual because of behavioural differences.[6]

18.2.1 Juveniles

The primary sex ratio represents that at conception,[7] and there are no such data for blue grouse, or most species. The secondary sex ratio, that at birth, is the first for which data are available for blue grouse.

(a) *Secondary sex ratios*. Only limited information is available on sex ratios at birth, all from Vancouver Island. Here, 172 eggs were collected from nests, incubated artificially, and the chicks raised in an aviary. There were 83 males and 89 females among these birds,[8] not different from a ratio of 1:1 (Zwickel and Bendell 1967*b*). Also, 182 young chicks, most <7 days of age (all <10 days of age), were brought into our aviary from the wild. Among these were 92 males and 90 females, not different from the ratio for those hatched from eggs or from 1:1. Nor did the combined sample of 175 males and 179 females differ from 1:1. Within this group, 88 males and 90 females died by about 1 September of their first year, suggesting no differential mortality up to that time under conditions in the aviary.

(b) *Tertiary sex ratios*. More information is available on tertiary sex ratios, those of larger juveniles in mid to late summer.[9] Data are available from birds collected or banded in the field, shot by hunters, or in museum collections.

The first sex ratio data for juveniles were provided by Bendell (1955*b*) at Lower Quinsam. He collected 70 males and 68 females between 15 June and 15 August in 1951 and 1952. These birds ranged from downy young to ~9 weeks of age, and the ratio did not differ from 1:1.

At Comox Burn and Hardwicke Island we placed patagial wing tags on large numbers of young grouse prior to when we could identify sexes. Wing tags were applied at ages ranging from newly hatched to ~4 weeks of age. Many of these birds were recaptured, resighted, or shot by hunters at a later date, by which time sexes could be identified. Sex ratios of these birds did not differ among years at either area, so these data were combined within areas (Table 18.3). The ratio for chicks at Comox Burn differed from 1:1 but that at Hardwicke Island did not [1a, b], and those for the two areas did not differ from each other [1c]. The combined ratio for both areas differed from 1:1 [1d] and, along with the individual samples, suggested a deficiency of males. These data were biased toward females, however, because sexes sometimes were not determined until birds were captured as yearlings or adults. Since yearling males are mostly non-breeders, they were less likely to be captured than yearling females. Thus, sexes of more wing-tagged males were determined as adults than as yearlings (when compared to females) and by which time some mortality between the first and second years had occurred. We suspect no difference from a 1:1 ratio among wing-tagged chicks if we could have corrected for this bias.

Sex ratios of leg-banded chicks did not differ among years at either Comox Burn or Hardwicke Island, so these data were combined within areas (Table 18.3). Ratios were balanced at both areas and for the two samples combined [2a–c].

One large sample of leg-banded chicks is available for an interior population. Standing (1960), Henderson (1960), Bauer (1962), and we marked 523 juveniles on the Methow Game

Table 18.3. Sex and sex ratios of wing-tagged and leg-banded juveniles at Comox Burn and Hardwicke Island.

	No. marked		Males/
	Male	Female	female
WING-TAGGED			
Comox Burn (1972–1977)	68	97	0.70
Hardwicke Island (1979–1984)	174	194	0.90
Total	242	291	0.83
LEG-BANDED[a]			
Comox Burn (1972–1978)[b]	151	162	0.93
Hardwicke Island (1979–1984)	445	447	0.99
Total	596	609	0.98

[a] Sex was determined on the basis of upper tail coverts (Nietfeld and Zwickel 1983) at ages ranging from ~6 to 15 weeks of age.

[b] Data from Nietfeld and Zwickel (1983).

Table 18.4. Sex and sex ratios of juveniles killed by hunters.

	No. examined		Males/
	Male	Female	female
VANCOUVER ISLAND			
Campbell River (1962–1964)	220	152	1.45
Copper Canyon (1964)	160	165	0.97
Ash River (1964)[a]	56	49	1.14
Courtenay (1970–1979)[b]	522	529	0.99
Cumberland (1972)[c]	31	24	1.29
INTERIOR POPULATIONS			
Chumstick (1953–1964)[d]	351	399	0.88
Conconully (1953–1964)[d]	788	964	0.82
Eight Mile Creek (1959–1961)	40	45	0.89
Middle Park (1975–1982)[e]	1320	1212	1.09
(1975–1977, 1979–1982)[e]	955	925	1.03

Note: All data collected at checking stations except those from Middle Park, where 87% were collected at volunteer wing collection stations, 12% at checking stations, and 1% by mail-in wing surveys (Hoffman 1985).

[a] Samples collected by BR Simard.

[b] From Zwickel (1982); no data for 1974 because of fire closure.

[c] Samples collected by JD Vanada.

[d] From Zwickel et al. (1975).

[e] From Hoffman (1985).

Range—mid to late summer in the years 1955–1961. There were no differences in sex ratios among years. The composite ratio for all years, 266 males:257 females, was balanced [3].

Other samples are of juveniles shot by hunters (Table 18.4). These are more age and time specific than from banded birds.[10,11] Among five sets of data from Vancouver Island, in only one case (Campbell River) did the sex ratio differ from 1:1 [4a–e]. Data from Courtenay represent collections from 9 years, with no annual sample differing from 1:1 (Zwickel 1982). Unbalanced ratios at Campbell River are from 3 years only, with no difference among samples and all suggesting a deficiency of females. We doubt that hunter selection will explain this deficiency because juveniles there were relatively young when shot, with dimorphic sex characteristics only beginning to appear. Nor will differential migration of males and females explain it, for samples were collected before most migration of juveniles (Bendell and Elliott 1967), and because no deficiencies were apparent at other areas of Vancouver Island in the same years. Populations had been declining in the Campbell River region for the previous 7–8 years, but whether this influenced juvenile sex ratios there is not known.

Among interior hunting samples (Table 18.4), juvenile ratios at Conconully and Middle Park differed significantly from 1:1 and that at Chumstick was nearly different [5a–d]. Males appeared deficient at Chumstick and Conconully, females, at Middle Park. In 8 years of data from Middle Park, however, only one annual sample (1978) differed from 1:1. If this sample is excluded, the combined sample for the other 7 years is not unbalanced [5e]. We think all interior samples are potentially subject to the bias of differential migration and (or) habitat selection, either of which might also differ among years. Among 12 annual samples at each of Chumstick and Concounully, in only 2 at Chumstick and 4 at Conconully were ratios unbalanced (Zwickel et al. 1975). Samples from Eight Mile Creek were balanced in all years. Hartkorn (1957) also reported a balanced sex ratio among juveniles shot by hunters in Montana ($n = 469$). Most evidence suggests juvenile ratios in autumn are balanced, with the principal exception from Campbell River and for which we see no clear explanation.

Specimens in museum collections were also used to examine sex ratios (see 3.4). We chose birds from the period 1 September to 31 December as representing the time when collector's biases should be minimal.

The combined sample of juveniles for coastal races, *D.o. fuliginosus*, *D.o. sitkensis*, *D.o. sierrae*, and *D.o. howardi*, 71 males and 93 females, was not different from 1:1 [6a]. That for interior races, *D.o. obscurus*, *D.o. oreinus*, *D.o. pallidus*, and *D.o. richardsonii*, included 119 males and 146 females, not different from 1:1 [6b]. The two samples did not differ from each other but when combined (190:239) did differ from 1:1 [6c], suggesting a deficiency of males. Differential migration (Jamieson and Zwickel 1983*a*; Hines 1986*b*), and (or) differential habitat selection by young males and females, may explain the deviation from 1:1 in this sample.

18.2.2 Yearlings

By our classification, juveniles become yearlings on 1 January of their first year of life. This age class of birds is important at the population level, as they provide replacements for breeding birds that die. They can be identified as yearlings until they lose all primaries in their first postnuptial moult.[12]

(a) *Field studies*. Our samples of yearlings from field studies are from breeding areas, beginning in March, and mainly from British Columbia. On breeding range, yearlings present special biases because most males do not hold territory, tend to be secretive, and begin returning to winter range in mid to late June (see 17.1.4). In contrast, many yearling females breed, are readily captured or identified from bands once with brood, and if successful at raising chicks, remain on breeding range through much of the summer. As well, in both sexes there may be non-breeding birds (Zwickel 1980) in which behaviour and observability differ from those that breed. To minimize potential biases, we examined sex ratios of yearlings for birds from Vancouver and Hardwicke islands for the period from March until the first hatch of a nest of a yearling female each year[13] (Table 18.5).

There were no differences in sex ratios of yearlings at Comox Burn$_{\text{cp}}$ or Hardwicke Island among years, so samples were combined within areas (Table 18.5). At neither area did the composite ratio differ from 1:1 [7a, b]. Nor did that for data for 4 years from Ash River (Redfield 1973*a*) [7c]. Samples from all three areas had more females than males, and when those from all areas were combined, the sex ratio approached, but did not reach, a significant difference from 1:1 [7d]. We suspect the tendency toward more females than males is explained by differences in behaviour and that the true sex ratio in this age class is balanced. Support for this contention comes from two removal experiments. Virtually all grouse were shot on a removal plot at Middle Quinsam in 1970, with 22 male and 13 female yearlings removed (Bendell et al. 1972), not different from 1:1 [8a]. Virtually all grouse were captured alive for transplanting, or shot, at our removal

Table 18.5. Sex and sex ratios of yearlings captured and (or) sighted prior to first hatch by a yearling female each year at Comox Burn$_{cp}$, Hardwicke Island, and Ash River.

	No. identified		Males/
	Male	Female	female
Comox Burn$_{cp}$ (1962–1964, 1969–1977)	146	160	0.91
Hardwicke Island (1979–1984)	97	109	0.89
Ash River (1968–1971)[a]	121	142	0.85
Total	364	411	0.89

[a] Includes captured birds only, data from Redfield (1973*a*).

plot at Comox Burn, Tsolum Main. The 31 male and 33 female yearlings that were removed (Zwickel 1972*a*) did not differ from 1:1 [8b]. These studies indicated that yearlings of both sexes were present on breeding areas in approximately equal numbers.

Wing et al. (1940) reported that more young females than males may come onto breeding range in spring, for in north-central Washington they found large numbers of what they thought were non-breeding yearling males, but no females, in subalpine habitats in midsummer. They could not, however, rule out that these birds had moved there from lower elevations by the time they sampled this population. Evidence from radio-marked birds (Sopuck 1979) indicates that this is likely. Another possibility is that males and females there may have been using different habitats.

In contrast to our findings, Boag (1966) captured 25 male and 61 female yearlings (0.41:1) at Sheep River (1955–1962), a significant deviation from 1:1 [9a]. He suggested no difference in catchability of young males and females and considered this a true difference in the proportions of the two sexes. His sample, however, was collected throughout spring and summer and does not include any consideration of the now documented differential behaviour and migration of males and females. Our banding samples for the entire field seasons at Comox Burn$_{cp}$ (1969–1978) and Hardwicke Island (1979–1984), 136 males:277 females (0.49 males/female) and 74 males:234 females (0.32 males/female), respectively, also were heavily biased toward females and bracket the 8-year sample from Sheep River. Most of the difference between males and females in our sample is due to availability, observability, and catchability. Yearling females are available for a longer time than males, and those with broods are more catchable, and their bands more easily read, than the more secretive males. We suspect the sex ratio of yearlings at Sheep River was not as unbalanced as Boag's data indicate.

(b) *Samples from hunters*. Grouse shot by hunters (Table 18.6) do not show the same balance among yearlings as indicated for birds on breeding range. Three samples from Vancouver Island and two of three from interior populations had a significant excess of females in the kill, and the third interior population, though the sample is not significantly different from 1:1, had a similar trend [10a–f]. Vancouver Island samples showed the greatest imbalance, and we believe this resulted mainly from earlier migration of yearling males than females from summer range, coupled with the relative inaccessibility of wintering areas to hunters, i.e., the difference reflects availability. Since Vancouver Island samples were collected in late August and early September, differential timing of moult of males and females is likely not greatly involved in causing the difference, i.e., most yearlings should still have been identifiable as such.

Table 18.6. Sex and sex ratios of yearlings killed by hunters.

	No. examined		Males/
	Male	Female	female
VANCOUVER ISLAND			
Campbell River (1962–1964)	5	45	0.11
Courtenay (1970–1979)[a]	12	146	0.08
Chemainus River (1964)	7	43	0.16
INTERIOR POPULATIONS			
Chumstick (1953–1964)[b]	23	35	0.66
Conconully (1953–1964)[b]	39	107	0.36
Middle Park (1975–1982)[c]	176	241	0.73

Note: All data were collected at checking stations except those from Middle Park, where 87% were collected at volunteer wing collection stations, 12% at checking stations, and 1% by mail-in wing survey (Hoffman 1985).

[a] From Zwickel (1982); no data for 1974 because of fire closure.

[b] From Zwickel et al. (1975).

[c] From Hoffman (1985).

Winter areas of interior birds for which data are available (Table 18.6) are much more accessible to hunters than those on Vancouver Island (but not equally so in each area) owing to an elaborate system of forestry roads. In these samples, especially at Chumstick and Middle Park, much of the imbalance among yearlings likely resulted from differential moult (owing to relatively late collections more males than females were potentially classified as adults). At Conconully, where the greatest imbalance was found, access to wintering areas is more restricted (Zwickel et al. 1975). There, differential moult and (or) access for hunters likely contributed to the difference.[14]

In summary, unbalanced sex ratios among yearlings killed by hunters are most easily explained by differential moult, migration, and behaviour; timing of collections; and accessibility to hunters, acting alone or together. Relative impacts of each may vary among populations.

18.2.3 Adults

Adult includes all grouse ≥2 years of age, although by 1 September it may include some yearlings (see above), and by 1 October would include most yearlings. Information on sex ratios of adults comes from removal studies, census data, banding samples, and hunting harvests. Total removal studies provide the most reliable data and census estimates in which a large proportion of both sexes is banded, the next most reliable.[15]

(a) *Removal studies*. Our attempts to remove all blue grouse from two areas provide the only information on adult sex ratios from removal studies. At Middle Quinsam, Bendell et al. (1972) shot 42 male and 30 female adults on a 365-ha experimental plot in 1970. In the same year, 62 adult males and 63 adult females were removed from Tsolum Main, the 625-ha removal plot at Comox Burn (Zwickel 1972*a*). Neither sample differed from 1:1 [11a, b].

(b) *Census estimates*. At Comox Burn$_{cp}$, where most birds were marked, sex ratios of adults did not differ among the years 1969–1977.[16] Combined data for all years showed significantly more males (*n* = 764) than females (*n* = 676) [12a]. At Hardwicke Island, also with most birds marked, there was no difference among the years 1980–1984 (data for 1979 excluded because of an incomplete census of adult males). Combined data for these years show significantly more females (*n* = 779) than males (*n* = 594) [12b]. The contrast between areas will be considered below (see 18.2.4).

Redfield's (1973) census data from Ash River indicated no differences in adults among the years 1968–1971 (calculated by us from data in his Table 3). Data for all years combined totalled 399 males:452 females, more females than males, but not quite significantly so [13].

Boag (1966) marked 108 adult males and 149 adult females at Sheep River between 1955 and 1962, significantly more females than males. In the first 4 years of study, he had a very small proportion of his territorial males marked (17%–33% in 3 years and incomplete data for the fourth). The proportion of marked females was unknown. This sample may not represent the true sex ratio of adults in that population.

(c) *Hunting samples*. As with yearlings, sex ratios among adults shot by hunters show much variation (Table 18.7). Hatter (1955) first pointed out a great deficiency of adult males in the kill of blue grouse on Vancouver Island and related it to early migration of males from breeding range and relative inaccessibility of wintering areas to hunters. Samples from Courtenay are from Comox Burn and surrounding areas. Those from the breeding range at Comox Burn$_{cp}$ (see above) showed an excess of males in the population, the opposite of hunting samples. Clearly, the sex ratio among birds harvested by hunters represents availability rather than the true ratio in the population. All samples from hunters on Vancouver Island support this conclusion [14a–c and Zwickel 1982].

Table 18.7. Sex and sex ratios of adults killed by hunters.

	No. examined		Males/
	Male	Female	female
VANCOUVER ISLAND			
Campbell River (1962–1964)	3	143	0.02
Chemainus River (1964)	12	93	0.13
Ash River (1964)[a]	0	46	0.00
Courtenay (1970–1979)[b]	44	405	0.11
INTERIOR POPULATIONS			
Chumstick (1953–1964)[c]	191	171	1.12
Conconully (1953–1964)[c]	413	552	0.75
Eight Mile Creek (1959–1961)	27	22	1.23
Middle Park (1975–1982)[d]	863	835	1.06

Note: All data were collected at checking stations except those from Middle Park, where 87% were collected at volunteer wing collection stations, 12% at checking stations, and 1% by mail-in wing survey (Hoffman 1985).

[a] Samples collected by BR Simard.

[b] From Zwickel (1982); no data for 1974 because of fire closure.

[c] From Zwickel et al. (1975).

[d] From Hoffman (1985).

In interior populations, three of four samples indicated balanced sex ratios among adults [14d, e, and Zwickel 1975]. Only data from Conconully suggested a deficiency of males (Zwickel 1975). As noted, winter areas there are less accessible to hunters than at Chumstick, and this likely accounted for the difference between these areas. Wintering and breeding areas also appear more equally accessible at Eight Mile Creek and Middle Park than at Conconully.

Hartkorn (1957) noted a deficiency of adult females in a hunting sample in Montana (2.83 males:1 female, *n* = 153) and suggested females might have higher mortality than males. We suspect his sample was more likely biased by the relative accessibility of males and females to hunters. More recent data from Montana support this suggestion, for Mussehl (1963*b*) found adult males most prevalent in the harvest in eastern districts of Montana and females most prevalent in western districts. He related the difference to a greater accessibility of wintering areas in eastern districts.

In summary, among adults many of the differences in sex ratios of hunted birds appear related to differential distribution of males and females in autumn, in concert with differences in accessibility at local areas. Earlier moult of males also confounds the picture, for more yearling males than females may be classified as adults—how many is determined by local time of hatch and timing of hunting seasons. Autumn sex ratios of adults and yearlings derived from hunting samples likely seldom represent true ratios within given populations. These data, however, may have importance to biologists involved in manipulating harvests.

18.2.4 The breeding population

Sex ratios within specific age classes may be less important than the combined sex ratio within the breeding population, for a deficiency of adults may be compensated for by yearlings. Since many yearling females breed, it is pertinent to examine the sex ratio of the total breeding population.

Few workers have provided independent estimates of numbers of yearling and adult males and females from which the total sex ratio in the breeding population can be examined. The first such effort was for a relatively small plot at Lower Quinsam (Table 18.8). The ratio of males:females did not differ between 1951 and 1952, and the combined ratio did not differ from 1:1 [15a]. Nor was the ratio of males:females unbalanced among years at Ash River, Comox Burn$_{cp}$, or Green Mountain. In no case did the combined data for an area differ from 1:1 [15b–d]. At Comox Burn$_{cp}$, the deficiency of adult females (18.2.3) appears to have been compensated for by yearlings.[17] These data all suggest a balanced sex ratio among breeders. Until recently, Boag (1966) was the only worker to suggest the sex ratio in any breeding population, that at Sheep River, might not be balanced. But, his conclusion was based on banded birds only.

In contrast to the generalization drawn above, more recent study with the high-density, but declining, population at Hardwicke Island showed an imbalance in favour of females among adults plus yearlings in 1980, but one that steadily nar-

Table 18.8. Sex and sex ratios of adults plus yearlings on Vancouver Island and at Green Mt.

	No. of grouse		Males/
	Male	Female	female
VANCOUVER ISLAND			
Lower Quinsam (1951–1952)[a]	49	55	0.89
Ash River (1968–1971)[b]	863	903	0.96
Comox Burn$_{\text{cp}}$ (1969–1977)	1092[c]	1094	1.00
GREEN MT. (1976–1980)[d]	107	92	1.16

[a] From Bendell (1955*c*); yearling males estimated as 30% of total males.
[b] Data calculated from Table 3 of Redfield (1973).
[c] Yearling males estimated as 30% of total males.
[d] From Hoffman (1981).

rowed to a nearly balanced state in the moderately dense population in 1984 (Zwickel et al. 1988). Although we have some reservations about the reported unbalanced sex ratio in grouse at Sheep River (Boag 1966), the Hardwicke population also was declining.

In summary, although most yearling males do not breed, sex ratios among yearlings plus adults are usually balanced on breeding range. The only clear exception to this generalization was the declining, high-density (at start of study) population at Hardwicke Island. A caveat we must put on this conclusion is that there is no good method for identifying numbers of nonbreeders. We have no reason to believe sex ratios of nonbreeders would change the generalization, however, for approximately equal numbers of yearling males and females were found at Middle Quinsam and Tsolum Main in 1971 (Bendell et al. 1972*a*; Zwickel 1972*a*), the year of replacement following near-total removals in 1970. Many replacement birds presumably represented birds that would not have bred without removal of virtually all breeders in 1970. Overall, we believe sex ratios are usually balanced throughout the life of most populations, beginning at birth and continuing into adult stages.

18.3 Age structure

Age structure of a population can be viewed at different levels. If a population is stable over time (Hickey 1955) and juvenile, yearling, and adult age classes can be identified, age structure can be used to estimate average annual turnover within these groups. These data also may provide an index to productivity and survival, within or among populations. At a more detailed level, if all, or most, year classes can be identified, e.g., in extensively banded populations, one can estimate age-specific survivorship and life expectancies (Emmel 1976). Here, we examine age structures in spring and summer (yearlings:adults), and in autumn (juveniles:yearlings plus adults).

18.3.1 The breeding population—yearlings:adults

In a stable population, the proportion, or percentage, of yearlings among yearlings plus adults must at least equal the annual rate of mortality among adults and if so equates to annual turnover in the breeding population. This proportion signifies the minimum number of yearlings necessary to maintain stability. If the proportion of yearlings exceeds the adult mortality rate, the breeding population will either increase or some yearlings will disperse or not breed. Age structure has implications for studies of populations, behaviour, and habitat selection, among others.

(a) *Males.* Among males, the annual proportion of yearlings identified is erratic (Table 18.9) and seldom sufficient for replacement of adults that disappear (~30%/year (Zwickel et al. 1983)), even in stable populations. Variation in numbers identified at Comox Burn and Hardwicke Island (significant at both areas [16a, b]) may reflect differences in behaviour or, perhaps, differences in numbers of yearling males that come onto breeding range. That populations maintain stability despite a low proportion of yearlings identified suggests that some are missed. A principal exception to this generalization involves numbers of yearling males identified in removal studies. For example, in our total removal studies in 1970 (Bendell et al. 1972; Zwickel 1972*a*), 42 adult and 22 yearling males (34% yearling) and 62 adult and 31 yearling males (33% yearling) were taken from our experimental plots at Middle Quinsam and Tsolum Main, respectively. The Middle Quinsam population was declining slightly while that at Comox Burn$_{\text{cp}}$ was increasing. The numbers of yearling males removed were adequate at both areas for normal adult replacement. On the respective control plots only 23% (10/43) and 14% (10/72) yearling males were identified in that year. We take this as evidence that some yearling males are missed with normal census methods, consistent with what is known of their secretive behaviour (Sopuck 1979; Jamieson 1985). On breeding range, total removal experiments likely give the most reasonable estimates of numbers of yearlings among males.

Some samples are available for other coastal populations. Here, too, numbers of yearling males identified are often inconsistent with what is known of adult mortality. For example, in the very dense population at Lower Quinsam (1950–1952, cited in Bendell and Elliott (1967)) 82 adult and 10 yearling males (11% yearling) were shot or captured, fewer yearlings than needed to maintain the stability that was observed (Bendell 1955*c*). In the more sparse population at Middle Quinsam (1958–1962), Bendell and Elliott (1967) determined age for 223 adults and 55 yearlings (20% yearling), less than expected. At Ash River, Redfield (1974) banded 405 males (1968 to 1971), of which 144 were yearlings (36%). This was consistent with the mortality rate of adult males in this area, but that population was increasing. In a subalpine population on Vancouver Island, King (1971) estimated that 27% of the males were yearlings, approximately what one would predict for nearby lowland populations on the basis of adult mortality rates, but it is not clear how his estimate was derived.

Age structure among males on interior breeding range is available for only two populations. Standing (1960) collected 60 males in the Methow Valley between late February (one bird only) and August, 1956–1957. Of these, eight were yearlings (13%). Boag (1966) banded 133 males between 1955 and 1962 at Sheep River, of which 25 were yearlings (19%). The percentage yearlings in both samples was less than needed for replacement.

Table 18.9. Percent yearlings among banded adults and yearlings at Comox Burn$_{cp}$ and Hardwicke Island, by year.

	Male		Female	
	n	% yearlings	*n*	% yearlings
COMOX BURN$_{cp}$				
1969	74	26	65	43
1970	69	10	71	37
1971	110	34	101	50
1972	94	13	83	40
1973	97	29	93	41
1974	83	12	88	31
1975	68	16	82	51
1976	78	22	77	35
1977	77	9	63	22
1978	65	23	37	27
Total	815	20	760	39
HARDWICKE ISLAND				
1979	126	25	301	40
1980	167	28	276	32
1981	143	20	208	25
1982	120	21	162	26
1983	98	15	109	27
1984	69	12	84	30
Total	723	21	1140	31

(b) *Females*. We think most or all yearling females come onto breeding areas, and since many breed (and are captured and identified), age structure of females is not subject to the same biases as in males. Age structure among banded females (Table 18.9), as with males, differed among years at both Comox Burn$_{cp}$ and Hardwicke Island [17a, b]. Combined percent yearlings among females at Comox Burn$_{cp}$ was significantly higher than at Hardwicke Island [17c]. In total removal studies at Middle Quinsam (Bendell et al. 1972) and Comox Burn (Zwickel 1972*a*), 30 adult and 13 yearling females (30% yearling) and 63 adult and 33 yearling females (34% yearling) were removed from the respective experimental plots, not different between areas [18a]. At neither area did the percent yearling females on control plots (Middle Quinsam, 39%, 16/41; Comox Burn$_{cp}$, 37%, 26/71) differ from that of removed birds at the respective areas [18b, c].

More comparative age structure data are available for females (Table 18.10) than for males. Among seven samples tested for annual variations, only at Middle Quinsam, Sheep River, and the Methow Game Range were no differences found [17a, b, 19a–e]. The Middle Quinsam sample represents only 4 years, and some annual samples for Sheep River and the Methow Game Range were very small. It seems clear that age structure often varies among years in females on breeding range. Differences within areas may reflect, at least in part, the previous year's production (Zwickel 1980). In summary, data from females on breeding range indicate that yearlings usually represent ~25–40% of females identified.[18]

We also examined age structure of females among museum specimens. We included all females collected between 1 January and 31 August.[19] Among 223 coastal females (*D.o. fuliginosus*, *D.o. sitkensis*, *D.o. sierrae*, and *D.o. howardi* combined), 75 (34%) were yearlings, and among 264 interior females (*D.o. obscurus*, *D.o. oreinus*, *D.o. pallidus*, and *D.o. richardsonii* combined), 91 (35%) were yearlings. There was no statistical difference between the two groups [20], suggesting similar age structures in coastal and interior females. The percentage yearlings within these samples are well within the range of those from the more area-specific studies considered above. A similar analysis cannot be done for males because of potential collection biases associated with singing (mostly adults) and silent (most yearlings) birds in spring and summer.

18.3.2 Age structure in autumn—juveniles: yearlings plus adults

Age structure in autumn provides an estimate of turnover from one autumn to the next. Birds killed by hunters have pro-

Table 18.10. Percent yearlings among banded adult and yearling females on various breeding ranges.

	n	% yearlings	Range	Source
COASTAL BRITISH COLUMBIA				
Lower Quinsam (1950–1952)	152	22	—	Bendell and Elliott 1967
Middle Quinsam (1959–1962)	283	37	31–44	Bendell and Elliott 1967
Ash River (1968–1971)	664	49	40–57	Redfield 1973
Comox Burn$_{cp}$ (1969–1978)	760	39	22–51	This study
Hardwicke Island (1979–1984)	1140	31	25–40	This study
INTERIOR POPULATIONS				
Sheep River (1955–1962)	210	29	13–46	Boag 1966
Methow Game Range (1957–1961)[a]	132	25	—	This study
Methow Game Range (1968)[a]	43	21	—	This study
Skalkaho (1962–1967)	191	27	6–38	Schladweiler 1968
Skalkaho (1986)	37	35	—	This study
Hudson Bay Mt. (1986)	29	41	—	This study

[a] Methow Game Range and vicinity, including Frazer Creek study area. Includes birds marked by Standing (1960), Henderson (1960), Bauer (1962), and ourselves.

Table 18.11. Percent juveniles among weighted adults[a] plus juveniles killed by hunters in autumn.[b]

	n	% juveniles	Range	Sources
VANCOUVER ISLAND				
Campbell River (1962–1964)	755	50	50–51	This study
Copper Canyon (1964)	617	53	—	This study
Ash River (1964)[c]	211	47	—	This study
Courtenay (1970–1979)	2267	51	34–61	Zwickel 1982
Cumberland (1972)[d]	89	62	—	This study
Grand total (Vancouver Island)	3939	51	34–61	
INTERIOR POPULATIONS				
Chumstick (1953–1964)	1092	69	57–83	Zwickel et al. 1975
Conconully (1953–1964)	2856	61	53–71	Zwickel et al. 1975
Eight Mile Creek (1959–1961)	149	58	44–70	This study
Middle Park (1975–1982)[e]	4684	54	40–67	Hoffman 1985
Idaho (1952–1954, 1958)[f]	2332	60	53–71	Heebner and Dalke 1955, Salter 1954, Bizeau 1958
Montana (1957–1966)[g]	9721	63	58–79	Mussehl 1961, 1963*b*; Schladweiler 1968
Grand total (interior)	20 834	61	40–83	

[a] Numbers of adult plus yearling males adjusted to equal those of adult plus yearling females.

[b] Except where noted all data are from checking station records.

[c] Samples collected by BR Simard.

[d] Samples collected by JD Vanada.

[e] 87% of samples from volunteer wing collections, 12% from checking stations, and 1% from mail-in survey.

[f] Samples from various checking stations in the state.

[g] 1957–1958 samples from Bridger Mts.; 1959 samples from Bridger and Judith Mts.; others, statewide.

vided large samples of such data for some areas, for periods up to 12 years.

We converted all hunting season samples to weighted percent juvenile[20] (Table 18.11) because of variations in availability of adult and yearling males to hunters among areas (see 18.2.2(b)). As well, since yearlings are moulting into adult plumage in autumn (some cannot be identified as yearlings), adults and yearlings were combined for these analyses.

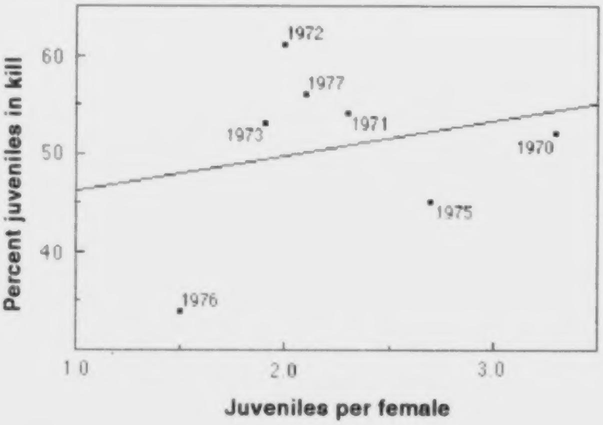
All hunting season samples for coastal birds are from Vancouver Island. Percentage juveniles was generally consistent among areas, at about 50%. The one exception, 62% at Cumberland, was computed from a relatively small sample. In the two areas with data for more than 1 year, there was no difference among years at Campbell River [21a], but there was a difference at Courtenay [21b].

Percentage juveniles in interior populations tends to be higher than for those from Vancouver Island, and all showed significant differences among years [21c–h]. Percentage juveniles for all Vancouver Island samples combined was significantly lower than for all interior samples combined [22]. These data provide evidence for variations in numbers of juveniles among years and indicate that coastal populations have proportionately fewer juveniles than interior populations in autumn. Although differential migration of juveniles, yearlings, and adults is possible, these data provide a general picture of age structures, especially in areas with several years' data.

Two other studies also suggest more juveniles among interior than coastal birds shot by hunters. Brown and Smith (1980) reported 69% juveniles in a sample from Arizona (139/201), and Cedarleaf et al. (1982) presented data for 6 years from northcentral Utah that averaged 63% juveniles. These are unadjusted data, for in neither case were they presented in a form that allowed weighting.

A number of workers have used juvenile ratios in the hunter-kill as estimates of, or indexes to, annual production of blue grouse (Redfield et al. 1970; Zwickel et al. 1975; Brown and Smith 1980; Cedarleaf et al. 1982; Zwickel 1982; Hoffman 1985). To test this procedure, we regressed percent juveniles in the kill at Courtenay (Zwickel 1982) on production estimates at Comox Burn_{cp} (Fig. 18.1), and the regression was

Fig. 18.1. Juveniles in the hunter-kill at Courtenay (in %) regressed on number of juveniles produced per female at Comox Burn_{cp}, 1970–1977 (no data for hunter-kill in 1974).



not significant [23]. This analysis indicated that kill data do not provide reliable estimates of production to autumn in blue grouse, for we believe data from breeding range are most indicative of production. Kill data are almost certainly affected by differential vulnerability of juveniles and adults to hunters among years, likely a reflection of differential migration and (or) dispersal, and perhaps, variations in weather as it might affect migration, dispersal, and hunting success.

We also examined museum specimens collected between 1 September and 31 December to evaluate autumn age structure. Among 282 coastal birds (weighted data^{21}), 164 (58%) were juveniles; among 413 interior birds, 265 (64%) were juveniles. The proportions of juveniles in these samples were in the same direction as for hunter samples, i.e., fewer juveniles in coastal than interior races, but were not significantly different [24]. More juveniles in interior than coastal populations in autumn might reflect the higher clutch sizes there (Table 10.14) and (or) lower mortality.

18.4 Survival

Annual survival, or its reciprocal, mortality, is an important attribute of a population from the standpoint of proximate trends within, or differences among, areas, and in terms of evolutionary relationships. While survival can be approximated from data on age structure, given certain assumptions, studies of banded individuals provide better estimates of this parameter.

Studies on Vancouver and Hardwicke islands involved intensive banding followed by intensive censusing in subsequent years. If birds present in year *n* are identified the next year, then a count of those seen in year *n* + 1 divided by the number present in year *n* should approximate annual survival. There are, however, potential biases in calculating survival in this way because of differences in the probability of identifying birds in the different sex and age classes. Survival estimates will be minimal in any case, and if biases can be identified, they can be considered. Dispersal also may affect estimates of survival of banded birds but is likely of minimal importance in yearlings and adults (see 17.2.2).

18.4.1 Age-specific survival

We examined rates of return ("survival") of known-aged males and females by year classes at Comox Burn$_{cp}$ and Hardwicke Island (Table 18.12). Return of males at Comox Burn$_{cp}$ differed significantly among year classes [25a] but with removal of yearlings did not differ, although close [25b].^{22} Females, but with fewer ages represented, were not different among year classes [26].

Yearling males at Hardwicke Island also differed from older males [27a], which did not differ among year classes [27b].^{23} As at Comox Burn$_{cp}$, there was no difference among year classes of females [28]. Annual survival appears constant in male and female blue grouse ≥2 years of age, as suggested from earlier studies (Bendell 1955*c*; Bendell and Elliott 1967; Zwickel and Bendell 1967*b*) and for many other birds (Deevey 1947; Hickey 1952; Farner 1955).

Table 18.12. Age-specific annual survival (%) of males and females ≥1 year of age at Comox Burn$_{cp}$, 1962–1977, and Hardwicke Island, 1979–1984.

	Males		Females	
Age (years)	*n*	%	*n*	%
COMOX BURN$_{cp}$				
1	184	64	340	53
2	124	81	193	62
3	103	68	121	57
4	67	81	65	52
5	51	65	33	52
6	33	64	18	67
7	17	94	13	54
8	14	79	7	0
9	9	56	0	—
10	4	100	0	—
11	3	67	0	—
12	2	0	0	—
Total	611	71	790	56
Total, ≥2 years old	427	74	450	57
HARDWICKE ISLAND				
1	171	49	349	59
2	81	62	206	51
3	44	70	97	62
4	25	84	44	45
5	8	75	13	77
Total	329	58	709	56
Total, ≥2 years old	158	70	360	54

18.4.2 Annual survival of yearling and adult males and females

No published survival data for blue grouse have been tested, or corrected, for detectability biases (e.g., differences in behaviour among individuals or populations), and the potential for such biases has apparently not been recognized, or acknowledged. In view of such biases among sex and age classes and study areas, uncorrected estimates from reidentification of banded birds may underestimate survival. Despite this problem, such data allow comparisons within and among areas. Here we use birds first banded as adults as well as those for which age in years was known.

(a) *Vancouver Island populations.* Bendell (1955*c*) provided the first information on survival of blue grouse from banded birds. He found no difference in survival of adult males among years at Lower Quinsam from 1950 to 1953. Data for all years combined showed a 69% (53/77) annual survival, and he assumed a similar rate for adult females. Later studies at Middle Quinsam (1959–1962) provided a statistically similar survival for adult males, 74% (103/140), that did not differ among years (Bendell and Elliott 1967). Bendell and Elliott concluded that the death rate of adult males was independent of age, year, and population density at these two areas. They also reported a 72% (21/29) survival of yearling males at Middle Quinsam, statistically identical to that of adult males. A small sample of banded adult females provided an estimate of 67% (10/15) survival for these birds, not different from that of adult males.

In early studies at Comox Burn$_{cp}$, 1962–1964, no differences were found in annual survival rates between yearling and adult males, yearling and adult females, or among years in any of these categories (Zwickel and Bendell 1967*b*). Combined data for all males and all females gave survival estimates of 75% (51/68) and 72% (48/67), respectively, not different from each other. Thus, up to this time, data from studies on Vancouver Island suggested constant survival among years and high and similar survival in males and females >1 year of age.

Redfield's (1975) studies at Ash River provided other estimates for grouse from Vancouver Island. He found no differences among years for yearling males, adult males, yearling females, or adult females. Average annual survival of yearling males (50%, 29/58) was lower than in adults (66%,104/157) [29a], but that for yearling females (40%, 72/179) was not different than in adult females (41%, 91/222) [29b].[24] Survival of yearling plus adult females was lower than in adult males [29c], a contrast to results from our earlier studies.

We think Redfield's results may have been influenced by his working three non-contiguous and relatively small study areas, which increases edge effect. This can potentially affect detectability of the relatively mobile females and yearling males more strongly than the more sedentary adult males. The Ash River study areas, and surrounding environs, also consisted of a patchwork logging pattern which included freshly logged areas each year. This too may have confounded survival estimates there, for banded birds had ready access to newly logged sites adjacent to the study areas. Survival data from Ash River may not be directly comparable to those from Lower Quinsam, Middle Quinsam, and Comox Burn.

The longest continuous sample of banded blue grouse from a single area is from Comox Burn$_{cp}$, 1969–1977 (Table 18.13).[25] There were no significant differences in rates of return among years for yearling males, adult males, and adult females [30a–c], but there was a difference in yearling females [31a]. The latter difference disappeared when data for 1976–1977 were deleted from the analysis [31b]. The low return in 1977 (as 2-year-olds) may relate to advancing forest succession and dispersal rather than survival. Overall, generally constant rates of return are consistent with results from earlier studies on Vancouver Island. Mean annual return of yearling males (62%) was lower than in adult males (73%) [32a], but those of yearling and adult females did not differ from each other [32b], with a mean for all females of 53%. Yearling and adult males returned at higher rates than all females combined [32c, d]. A lower rate of return of females than males as compared to the 1962–1964 period (72%) likely reflects a large increase in hunting pressure on this population in the latter period and will be considered in more detail in a future publication.

(b) *Hardwicke Island.* Here (Table 18.13), there were no differences in survival of yearling and adult males among years [33a, b], but a difference in both age classes of females [34a, b]. In yearling females there were no differences between the 1979 and 1980 cohorts, or among those for 1981, 1982, and 1983. Rate of return for the 1979 and 1980 cohorts (combined) indicated a higher survival than those for 1981, 1982, and 1983 (combined) [34c]. Deletion of the 1982 year class of adult females, eliminated the difference in that group. Thus, results from Hardwicke Island, except for yearling females

Table 18.13. Annual survival (%) of yearling and adult males and females at Comox Burn$_{cp}$ and Hardwicke Island.

	Males				Females			
	Yearling		Adult		Yearling		Adult	
Year	*n*	%	*n*	%	*n*	%	*n*	%
COMOX BURN$_{cp}$								
1969–1970	23	48	54	70	36	39	69	49
1970–1971	16	75	59	76	29	66	58	53
1971–1972	32	59	72	69	53	57	62	44
1972–1973	16	50	89	67	28	50	70	63
1973–1974	26	69	79	71	45	62	75	56
1974–1975	12	75	93	73	27	41	73	55
1975–1976	13	85	74	78	38	42	66	53
1976–1977	13	46	76	80	26	31	67	64
All years	151	62	596	73	282	50	540	55
HARDWICKE ISLAND								
1979–1980	79	58	98	59	177	64	180	52
1980–1981	37	49	123	68	64	69	194	54
1981–1982	34	44	126	63	60	47	172	62
1982–1983	14	36	110	68	28	39	150	43
1983–1984	12	25	88	51	20	40	84	60
All years	176	49	545	63	349	59	780	54

and one of five year classes of adult females, agree with earlier indications that survival of yearlings and adults appears constant among years. The lower survival of yearlings in the last 3 years of study may be associated with the population decline there.

Mean annual survival of yearling males was lower than in adult males [35a], but those of yearling and adult females did not differ from each other, with a mean for all females of 55%. This was not different from that of yearling males [35b]. Adult males returned at a significantly higher rate than females [35c].

Mean returns of adult and yearling males were significantly lower at Hardwicke Island than at Comox Burn$_{cp}$ [36a, b], but yearling females returned at a higher rate at Hardwicke [36c]. There was no difference in returns of adult, or combined yearling and adult, females between the two areas. Some of these differences may relate to the declining population at Hardwicke as compared to the increasing and more stable population at Comox Burn$_{cp}$.

(c) *Interior populations.* Few survival data are available for interior blue grouse and, with one exception, represent adult males only. Schladweiler (1968) presented data on rates of return for banded adult males from the Skalkaho area and the West Fork of the Bitterroot Valley in western Montana, 1963–1967. Returns of 68% (65/95) at Skalkaho, and 73% (62/85) in the West Fork, did not differ from each other [37], for a combined return of 71% at the two areas. Martinka (1970) worked at Skalkaho from 1967 to 1969 and reported a 74% return of territorial males, but did not present the data on which this calculation was based. These returns are consistent with those for adult males from most coastal study areas.

The most comprehensive set of banding data for interior blue grouse is from Sheep River, 1955–1962 (Boag 1966). Boag documented returns of 31% (11/36) for yearling males, 52% (51/98) for adult males, 47% (54/115) for yearling females, and 39% (43/110) for adult females. He found no significant differences among these sex and age classes and computed an overall mean rate of return of 44%. The return of yearling males was lower than at Middle Quinsam and Comox Burn$_{cp}$ [38a, b] and approached significance for those at Hardwicke Island and Ash River [38c, d]. The return of adult males at Sheep River was lower than those from Montana (Skalkaho and Bitterroot Valley combined) and from Lower Quinsam, Middle Quinsam, Comox Burn$_{cp}$, Hardwicke Island, and Ash River [39a–f]. Returns of yearling and adult females tended to be lower, but were within the range of coastal birds. Relatively low returns at Sheep River might reflect lower detectability of birds in this population or that dogs were not used for search. As well, the Sheep River population was declining throughout the period of study.

18.4.3 Juveniles—first-year survival

First-year survival involves young of the year from time of hatch until birds return to a breeding range, by our definition, as yearlings. In most cases, this represents the period from some time in June of the year of hatch to April of the following year, a period of ~9–10 months. Calculation of survival rates from banded young is not as straightforward as for older age classes because this is the stage of life in which natal dispersal occurs. Since many birds may disperse beyond study area boundaries, and peripheral areas are usually searched less intensively, calculations reflect minimum survival.

Because of problems associated with separating mortality from dispersal, we examine first-year survival in three categories: (1) First-summer Survival, as indicated by the difference between mean size of clutch and late-summer brood size, (2) First-winter Survival, as estimated from late-summer production and subsequent spring recruitment, and (3) First-year Survival Estimated From Banded Birds, as determined from marked juveniles known to be alive as yearlings. Use of all three provides information on the timing of losses and insight into some of the potential biases.

(a) *First-summer survival.* Once the hatch is completed, the most common method of evaluating juvenile survival is by counting numbers of young in broods. Reliable brood counts are difficult to obtain for very small chicks, which often "freeze", or run and hide. By 4–5 weeks of age, however, chicks are strong flyers and more readily flushed and counted (Henderson 1960; Boag 1966; Harju 1974; pers. observ.). The difference between mean late-summer brood size and mean size of clutch likely provides the best estimate of first-summer survival but misses broods in which all chicks die. We think this is uncommon in most years.

Despite problems associated with changing vulnerability of chicks to being counted, some authors have attempted to examine summer survival based on changes in mean brood size. Bendell (1955*c*) reported no significant weekly change in mean brood sizes over summer at Lower Quinsam. We found a heavy mortality of young blue grouse in the first 2 weeks of life in parallel studies of wild and aviary birds at Comox Burn$_{cp}$ and Middle Quinsam (Zwickel and Bendell 1967*b*). Following this high "early mortality", mean brood sizes in successive periods, by age of chicks, suggested little loss through the rest of the summer and was consistent with survival of chicks in our aviary. These studies indicated that survival is good once chicks are >2 weeks of age.

Others, too, have reported little summer mortality as based on brood counts. Caswell (1954*b*), at Brownlee, and Henderson (1960), at Frazer Creek, found little or no change in size of broods after an initial early mortality, although Caswell thought relatively large late-summer counts might result from brood mixing. Data from Bauer (1962) indicated little change in brood size after mid July at Frazer Creek. He also thought an increase in size in mid August might have resulted from combining of broods. And Boag (1964), at Sheep River, reported only slight mortality of chicks after 5 weeks of age, the age at which he first considered brood counts reliable. In contrast, Wing et al. (1944) and Schottelius (1951*a*) concluded there was a general decline in brood size over summer in northcentral Washington, but we think their data are equivocal and do not necessarily support their conclusions.

Obviously, some chicks die throughout summer due to predation, disease, accidents, and perhaps their own viability, so mean brood size must decline. Most data from brood counts, however, suggest that beyond a relatively high early mortality in the first 2 weeks of life, the probability of survival is good into and including late summer. If true, variations in first-summer survival among years will be caused mainly by variations in early mortality. As noted, total brood losses are a problem in these analyses, and are not part of the equation when using only changes in brood size.

We examined variations in summer survival of juveniles among years at Comox Burn and Hardwicke Island by calculating the percentage of mean clutch size represented by late-summer brood size. This measure reflects losses from egg to late summer and includes those due to infertility and failure to hatch. Since we used mean clutch size at each area for all years combined (there were only small variations among years in clutch size, fertility, or hatchability; see 10.6.2–10.6.4), differences in survival reflect mainly brood sizes, which were clearly different among years (see 18.5.2). Variations in first-summer survival appear to have resulted mainly from death of chicks.

Summer survival ranged from 35% to 60% at Comox Burn and 23% to 52% at Hardwicke Island, with means of 51% and 39% at the two areas, respectively (Table 18.14). There was no clear temporal pattern at Comox Burn, but a steady decrease from 1979 to 1984 in the declining population at Hardwicke Island. Lower mean survival at Hardwicke Island would result partly from lower fertility and hatchability than at Comox Burn (see 10.6.3 and 10.6.4) and partly from survival of chicks. Total brood loss complicates this analysis.

Mean summer survival reported for blue grouse on Vancouver and Hardwicke islands seldom attained 50% (Table 18.15). A major exception, 79% at Copper Canyon, was from a short-term study, with no information provided on sample sizes.

Table 18.14. Juvenile survival over summer at Comox Burn and Hardwicke Island, as calculated from mean clutch[a] and late-summer brood sizes.[b]

Area, year	Mean brood size	Survival (%)
COMOX BURN		
1969	3.5	54
1970	3.9	60
1971	3.6	55
1972	3.2	49
1973	2.9	45
1974	3.6	55
1975	3.6	55
1976	2.3	35
1977	2.8	43
Mean, all years	3.3[c]	51
HARDWICKE ISLAND		
1979	2.9	52
1980	2.9	52
1981	2.4	43
1982	1.9	34
1983	1.7	30
1984	1.3	23
Mean, all years	2.2[c]	39

[a] Based on weighted mean clutch sizes of 6.5 eggs at Comox Burn and 5.6 eggs at Hardwicke Island (Zwickel et al. 1988).

[b] On or after 30 July at Comox Burn; on or after 23 July at Hardwicke Island.

[c] Calculated from annual means.

Table 18.15. Juvenile survival (%) over summer for Vancouver Island and interior populations, as calculated from mean clutch and late-summer brood sizes.

Area	Survival		Sources
	Mean	Range[a]	
VANCOUVER ISLAND			
Lower Quinsam	39	32–50 (3)	Bendell 1955*c*
Copper Canyon	79	76–81 (2)	Mossop 1971
Middle Quinsam	47	39–55 (2)	Mossop 1971
Comox Burn$_{cp}$	51	35–61 (13)	Zwickel and Bendell 1967*b*, Mossop 1971, this study
Hardwicke Island	39	23–52 (6)	This study
INTERIOR POPULATIONS			
Methow Game Range	51	43–64 (6)	Standing 1960, Henderson 1960, Bauer 1962
Sheep River	60	47–68 (8)	Boag 1966
Liberty	47	41–58 (3[b])	Weber 1975
Green Mt.	53	42–60 (6)	Hoffman 1981
Eiby Creek	65	44–78 (5)	Hoffman 1981

Note: Survival calculated by us from data in individual manuscripts.

[a] Years of data are in parentheses.

[b] Annual samples >10 only.

Most studies of interior blue grouse suggest a higher summer survival than in coastal populations (Table 18.15). With one exception, Liberty, UT (a short-term study), mean survival was always >50%. On average, these data indicate a higher loss of chicks over summer in coastal British Columbia than in interior populations.

(b) *First-winter survival.* Bendell (1955*c*) estimated winter survival of juveniles indirectly for birds at Lower Quinsam. He assumed a stable population, an adult mortality rate of 31%, a population in which 40% of the females were broodless by late summer, and a mean late-summer brood size of two chicks. From this, he estimated there would be a 47% loss of juveniles between autumn and spring and considered this a general picture for that area. We used similar procedures to estimate autumn to spring losses at Comox Burn$_{cp}$ (Zwickel and Bendell 1967*b*). We considered 50% of all females to be broodless by late summer and made estimates for each of the years 1962–1964, based on mean brood sizes at the end of each summer. Estimated losses were 46%, 59%, and 52%, respectively. Hoffman (1981) made such estimates for interior blue grouse at Green Mt. and Eiby Creek. He used similar procedures and calculated mean over-winter losses as 52% ($n_{\text{years}} = 6$) and 62% ($n_{\text{years}} = 4$) for these areas, respectively.

Numbers of broodless females in late summer are difficult to estimate because hens without chicks are more difficult to find and identify than those with broods (Bendell 1955*c*) and because some hens leave breeding range soon after losing all their young (Sopuck 1979). This makes estimates as above less than ideal. Sopuck (1979) found that 28% of 25 radio-tagged hens at Comox Burn (weighted heavily to yearlings) lost their broods in the first 10 days after hatch, after which time most were retained. At Hardwicke Island in 1983, among 36 radio-marked hens known to have produced broods, 2 were killed by predators, 1 was not found after her chicks hatched (she may have moved off the study area or been killed), and 22 (61%) retained their broods at last sighting (20 were last seen in August, usually at time of radio removal). This was a year of small brood size, so this figure likely represents a high loss of complete broods. We used 70% brood retention at Comox Burn (30% loss) and 60% brood retention at Hardwicke Island (40% loss) to make more refined estimates of autumn to spring losses for hypothetical stable populations at these areas.

If one begins with breeding populations of 100 males and 100 females at each area and applies population parameters for each area to these populations, the estimated autumn to spring loss of late-summer juveniles to maintain stability would be 64% at Comox Burn and 45% at Hardwicke Island (Table 18.16). These figures are within the range of those reported for Lower Quinsam, Middle Quinsam, and Comox Burn$_{\text{cp}}$ in earlier years (Zwickel and Bendell 1967*b*), and for the two Colorado populations. However, since the estimate for total brood loss at Hardwicke Island (40%) was likely near the high end of the range, in years when this mortality is less, over-winter loss would increase, and the proportion required for spring replacement would decrease. Also recall that parameters for Hardwicke Island were those associated with a declining, not a stable, population.

Table 18.16. Estimated winter loss of juveniles to maintain stability in populations at Comox Burn and Hardwicke Island.

	Comox Burn	Hardwicke Island
BREEDING POPULATION		
n_{males}	100	100
n_{females}	100	100
REPLACEMENT NEEDED$_{\text{year } N+1}$[a]	60	60
$n_{\text{females producing broods}}$[b]	72	84
$n_{\text{surviving broods, late summer}}$[c]	50	50
MEAN BROOD SIZE$_{\text{late summer}}$[d]	3.3	2.2
$n_{\text{juveniles, late summer}}$	165	110
AUTUMN TO SPRING LOSS TO MAINTAIN STABILITY (%)	64	45

[a] Based on yearling and adult mortality rates of ~30%.

[b] Combined data for all years for banded females at each area (see Table 18.18).

[c] Based on loss of all chicks by 30% of females producing broods at Comox Burn, and 40% at Hardwicke Island.

[d] Combined mean brood size for all years at each area (see Table 18.20); calculated from annual means.

Hines (1986*a*) studied winter survival of radio-marked juveniles more directly at Hardwicke Island from 1979 to 1983. He monitored large juveniles from late summer until the following spring, or time of death, whichever was earlier. He used two methods to estimate survival. His estimates indicated at least 21%–28% of males, and 28%–35% of females, survived to the following spring. Unfortunately, this picture is confounded because 38% (105/279) of his birds disappeared, with fates postulated, or unknown. Hines's (1986*a*) belief that many of these birds died (his Table 7.1) may or may not be true, for at least eight birds are known to have dispersed to the mainland, which was monitored only cursorily. Although his conclusion that the documented survival was insufficient for spring replacement in this population was consistent with its decline, the picture is muddied by the disappearance of so many birds. Among birds Hines was able to monitor, most mortality occurred in autumn.

(c) *First-year survival estimated from banded birds.* As noted, attempts to estimate survival of banded juveniles is confounded by dispersal. Other factors also limit the utility of this method. For example, young blue grouse will not retain adult-sized leg bands until at least 4 weeks of age, and most banding studies have been limited to birds of this age, or older. In some cases, juveniles have been marked with numbered bands or wing tags only, requiring their recapture or collection for reidentification. In other cases, subsequent follow-up of banded birds may have been inadequate. Estimates of juvenile survival from return and recovery rates to breeding range must be minimal in all studies.

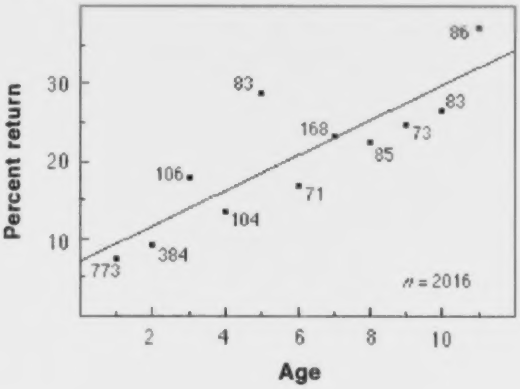
Bendell (1955*c*) was first to band young blue grouse. He marked 37 juveniles at Lower Quinsam in 1951 and 1952 and found none on summer range in subsequent years. He speculated that the lack of returns or recoveries might reflect emigration, high juvenile mortality, and (or) that birds may have been marked away from, but returned in later years to, natal areas outside his census plots. Bendell and Elliott (1967) marked 250 juveniles at Middle Quinsam. They resighted only five (2%) of these birds in later years and considered the low rate of return as evidence of death and dispersal. Boag (1966) marked 86 juveniles at 5–10 weeks of age at Sheep River and recorded a 4.7% return, too low to sustain his population. He considered this as evidence of dispersal more than mortality. Up to this time, indications were that return of young to areas where raised was very low and that this might be explained by high mortality and (or) dispersal. Low returns discouraged some workers from putting greater effort into juvenile marking programs.

Beginning in 1969, we initiated a more intensive juvenile banding program at Comox Burn. In 1972, we also began marking chicks between 2 weeks of age and the age at which they could be banded (~4 weeks) with patagial wing tags, and in 1973, all chicks too small to hold leg bands. Of 1958 birds wing-tagged or leg-banded between 1969 and 1976, 14% (n = 274) are known to have survived to at least yearling age, >93% of which were reidentified by us on our study areas (Zwickel 1983). This return was much higher than reported for any other population, even though it included many chicks marked in their first week of life.

This intensive wing-tagging and banding program allowed us to examine rates of return by weekly age classes. There was a steady increase in rate of return of chicks marked at 1 week (6%) to 10 weeks (41%) of age. Those >8 weeks old returned at a rate of ~40% (Zwickel 1983), very much higher than recorded in other studies.

We also marked large numbers of juveniles at Hardwicke Island from 1979 to 1984. Of 2016 wing-tagged or banded between 1979 and 1983, at least 14% (n = 292) survived to at least 1 year of age, most of which were reobserved by us on

Fig. 18.2. Return of wing-tagged and banded juveniles as yearlings or adults (in %) at Hardwicke Island as related to age (weeks) when marked, 1979–1984.



our study areas. This return was identical to that at Comox Burn but may be biased upward by some birds having been reobserved because they had been equipped with radios (Hines and Zwickel 1985). However, only 70 of 293 radio-marked juveniles, 24%, were identified as over-winter survivors (Hines 1986*a*), most of which also were identified by normal census methods in year *n* + 1. Such bias, if present, is small.

As at Comox Burn, chicks at Hardwicke Island showed a steady, and significant, increase in rate of return by age at time of marking (Fig. 18.2) [40], from 8% at week 1, to 37% for birds ≥11 weeks of age. Nine and 10-week-old birds returned at a rate of 26%, significantly lower than the 40% recorded for those of similar age at Comox Burn [41a]. At Hardwicke, we banded 86 chicks ≥11 weeks old. Their return, 40%, was not different from that of 9- and 10-week-old birds at Comox Burn [41b].

These data conflict with those from brood counts that indicate a high summer survival after a short period of high early mortality. The banding data are most robust and those based on brood counts have more potential for bias, e.g., problems associated with total loss of broods and brood mixing at older ages.

18.4.4 Longevity

Blue grouse are among the most long-lived of all grouse. Although Johnsgard (1983) reported only four tetraonines that reached ≥10 years of age (three capercaillie and one ruffed grouse), at least 14 blue grouse have attained this age (Zwickel et al. 1989). The oldest known longevity for any grouse is 15 years, a male white-tailed ptarmigan in Colorado (Braun et al. 1993). The second oldest was a male blue grouse (≥14 years of age) at Sheep River (Zwickel et al. 1989). Twelve males at Comox Burn or Middle Quinsam were ≥10 years old when last seen or killed; the oldest were 12 (*n* = 2).

At Comox Burn$_{cp}$, where we had nearly continuous study from 1962 to 1979, we identified three males ≥10 years old, three ≥11 years old, and one 12 years old. These were among 120 males that might have survived to at least 13 years of age, suggesting 12 may be at, or near, the maximum longevity to be expected for males on Vancouver Island (Zwickel et al. 1988). The oldest females recorded at Comox Burn were two ≥8 years of age, three ≥9 years of age, and one 11 years of age. The smaller number of females than males found in the older age classes may relate to a higher mortality rate and (or) a lower probability of detection among females than males (Zwickel et al. 1989).

18.5 Production

Breeding populations expand or contract as a balance among births, deaths, emigration, and immigration. Here we consider production as the number of young raised to late summer, just prior to the time when hens and chicks begin to leave breeding range and when broods begin to disband and chicks disperse. This is the equivalent of production at time of fledging in altricial birds. It reflects the number of females successful in raising a brood and the number of chicks that survive to late summer. These factors may be affected by age structure of the breeding population and may vary among years and areas.

18.5.1 Number of females with brood[26]

(a) *Age-specific*. We examined breeding success [defined here as having produced a brood] of known-aged females (age known to year class) at Comox Burn and Hardwicke Island (Table 18.17).[27] There was a significant difference among age classes at both areas [42a, b], but within areas, no difference when yearlings were excluded [42c, d]. Thus, within areas, fewer yearlings than adults were found with brood, but beyond 1 year females of all ages were equally successful. Percent yearlings with brood was less at Comox Burn than at Hardwicke Island [43a], but that for adults was not [43b], with a grand mean of 83% for adults (areas combined).

(b) *Among years*. Many birds are banded as adults, and their specific age is not known. Since there appears to be no difference among adult year classes in producing broods, we combined data for all adults to examine for differences among years. At Comox Burn$_{cp}$ (Fig. 18.3),[27] yearlings were different among years [44a], adults were not [44b], and both age class-

Table 18.17. Percentage of banded females known to be with brood by age in years, Comox Burn, 1969–1978, and Hardwicke Island, 1979–1984.

	Comox Burn		Hardwicke Island	
Age in years	*n*	%	*n*	%
1	289	53	323	73
2	9	81	89	89
3	62	77	81	81
4	33	88	65	88
5	[illegible]	100	39	82
6	[illegible]	67	26	81
7	8	63		
8	4	75		
COMOX BURN, adults 2–8 years	231	81		
HARDWICKE ISLAND, adults 2–6 years			300	85

Fig. 18.3. Banded females at Comox Burn known to be with brood (in %) for adults, yearlings, and age classes combined, 1969–1977. Means for each class are shown by arrows outside right borders. Numbers are annual sample sizes.

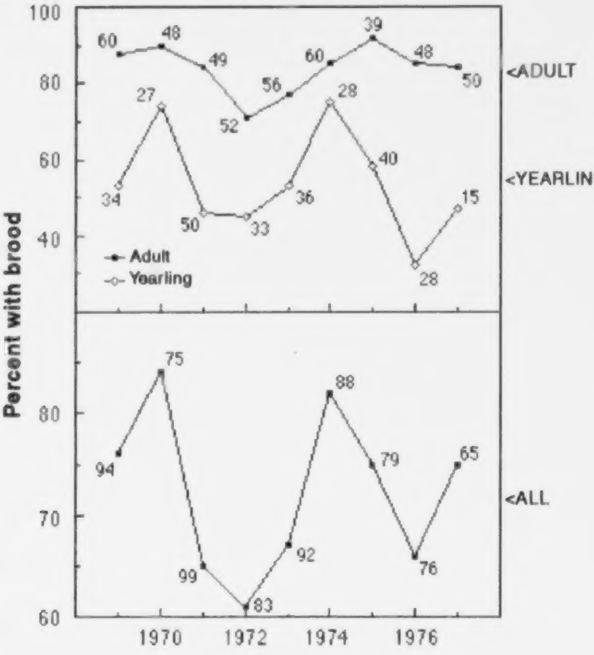
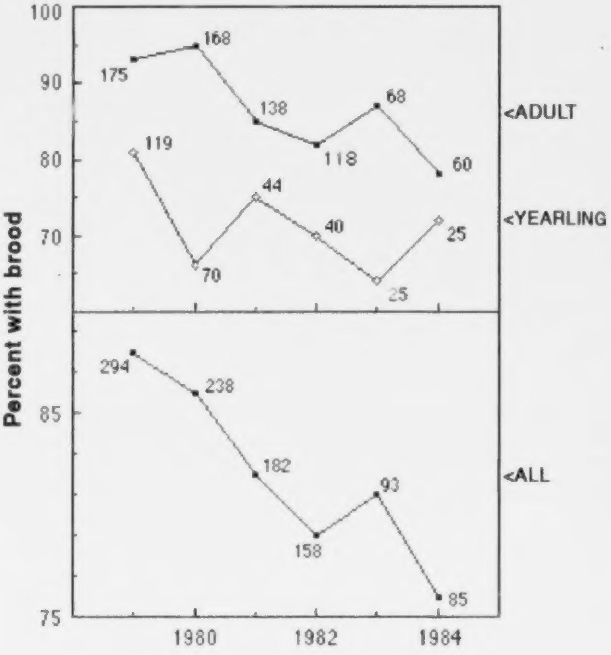


Fig. 18.4. Banded females at Hardwicke Island known to be with brood (in %) for adults, yearlings, and age classes combined, 1979–1984. Means for each class are shown by arrows outside right borders. Numbers are annual sample sizes.



es combined were different [44c]. At Hardwicke Island (Fig. 18.4),[27] there was no difference within yearlings [44d], a difference within adults [44e], and a near difference for age classes combined [44f]. Between 80% and 90% of adults produced broods in most years, >80% in 7 of 9 years at Comox Burn and 5 of 6 years at Hardwicke Island.

(c) *Among areas*. At Comox Burn$_{cp}$, significantly fewer yearling [43a], adult [45a], and all females combined [45b] produced broods than at Hardwicke Island (Table 18.18).[27] We think this larger sample for adults, which shows a significant 4% difference between areas should be accepted even though samples for known-aged adults (Table 18.17) [43b] were not different. Yearling females showed a 20% difference between the two areas, indicating they are the principal reason for the difference when all females are combined.

Some brood:broodless hen data are available for other populations but must be used with care, for the proportion of broodless hens identified may change in the course of the breeding season (Harju 1974; Hoffman 1981).[28] Although there are potential biases in such data, we examine what has been reported for other populations.

Bendell (1955*c*) estimated 40% of hens at Lower Quinsam were broodless. This was based on a difference in the number of broodless hens seen per hour between spring and midsummer and included non-breeders (if present), and unsuccessful breeders. We estimated ≤50% broodless females for our early studies at Comox Burn$_{cp}$ (Zwickel and Bendell 1967*b*). This was based on the number of banded hens with brood and the proportion of all hens sighted in July that were with brood; it, too, included non-breeders and unsuccessful breeders. At Ash River, 1968–1971, 70% of all banded yearlings (n = 323) and 84% of all banded adults (n = 335) produced broods (Redfield 1975). These data are directly comparable to those for Comox Burn$_{cp}$ (1969–1977) and Hardwicke Island, but are uncorrected for females that may have lost all chicks. The percentage of yearlings with brood was significantly higher than at Comox Burn$_{cp}$ [47a], but not different than at Hardwicke [47b]. That for adults was not different from that at Comox Burn$_{cp}$ [47c] or Hardwicke Island [47d]. These data suggest a clear difference in numbers of yearlings producing broods among areas (Comox Burn$_{cp}$ × Hardwicke Island × Ash River), but little difference in adults. We think differences among areas can be explained by a combination of variations in nesting success (high at Hardwicke Island, lower at Comox Burn and Ash River), amount of renesting by yearlings and adults (Sopuck and Zwickel 1983), and, at Ash River, by a high productivity of yearlings colonizing newly created habitats (Redfield 1975).

Table 18.18. Percentage of banded yearling and adult[a] females known to be with brood at Comox Burn$_{cp}$, 1969–1977, and Hardwicke Island, 1979–1984.

	Yearling		Adult		All	
	n	%	*n*	%	*n*	%
Comox Burn$_{cp}$	289	53	462	84	751	72
Hardwicke Island	323	73	727	88	1050	84

[a] Includes adults whose age to year class was not known.

Table 18.19. Late-summer brood sizes (mean ± SE)[a] of yearling, adult, and all females at Comox Burn, 1969–1977, and Hardwicke Island, 1979–1984.

	Comox Burn	Hardwicke Island
Yearling	3.2±0.25	1.9±0.31
Adult	3.4±0.18	2.4±0.26
All females	3.3±0.17	2.2±0.27

[a] Calculated from annual means (n_{years} CB = 9; n_{years} HI = 6).

18.5.2 Late-summer brood size[29]

(a) *Yearling and adult females*. Yearlings have smaller clutches than adults (10.6.2(a)), and other things being equal, they should have smaller late-summer brood sizes than older hens. Mean annual brood sizes of yearlings tended to be smaller than those of adults at Comox Burn and Hardwicke Island (Table 18.19), but not significantly so [48a, b]. Chicks of yearlings that retained broods to late summer survived at least as well as those of adults.

(b) *Variations among years*. There were significant differences in mean brood size among years at both Comox Burn and Hardwicke Island (Table 18.20) [49a, b]. All other studies with more than 2 years of data (Table 18.21) also suggest variations among years.

Table 18.20. Late-summer[a] brood sizes (mean ± SE) of all females, by year, at Comox Burn and Hardwicke Island.

Comox Burn			Hardwicke Island		
Year	*n*	Mean[b]	Year	*n*	Mean
1969	131	3.5±0.14	1979	426	2.9±0.08
1970	89	3.9±0.20	1980	290	2.9±0.10
1971	143	3.6±0.15	1981	206	2.4±0.09
1972	141	3.2±0.14	1982	99	1.9±0.10
1973	96	2.9±0.16	1983	96	1.7±0.10
1974	81	3.6±0.18	1984	24	1.3±0.13
1975	72	3.6±0.19	Grand mean[c]		2.2±0.27
1976	43	2.3±0.19			
1977	48	2.8±0.17			
Grand mean[c]		3.3±0.17			

[a] On or after 30 July at Comox Burn; on or after 23 July at Hardwicke Island.

[b] Includes broods from Comox Burn and Tsolum Main combined, except Comox Burn only in 1970 because of removal experiment.

[c] Calculated from annual means.

(c) *Variations among areas*. At Comox Burn$_{cp}$ yearling females, adult females, and all females combined had significantly larger late-summer broods than respective age classes at

Table 18.21. Late-summer brood sizes reported for coastal and interior blue grouse.

	Size of brood		
Area	Mean[a]	Range[b]	Sources
COASTAL SUBSPECIES			
Lower Quinsam	2.4	1.7–3.3 (5)	Fowle 1960, Bendell 1955*c*
Copper Canyon	4.9[c] (2)		Mossop 1971
Ash River	3.9	3.3–4.4 (4)	Redfield 1975
Middle Quinsam	2.7	2.2–3.7 (5)	Zwickel and Bendell 1967*b*, Ash 1979
Comox Burn$_{cp}$, 1963–1964	2.7	2.5–2.9 (2)	Zwickel and Bendell 1967*b*
1969–1977	3.3	2.3–3.9 (9)	This study
Hardwicke Island	2.2	1.3–2.9 (6)	This study
May Ranch	2.8 (1)		This study
INTERIOR SUBSPECIES			
Conconully	3.6 (1)		Wing et al. 1944
Sheep River	3.7	2.9–4.4 (8)	Boag 1966
Brownlee	4.3	3.6–4.9 (3)	Caswell 1954*b*, Heebner 1956
Frazer Creek	3.4	1.7–4.7 (7)	Standing 1960, Henderson 1960, Bauer 1960, this study
Montana	3.3[d] (10)		Hartkorn 1957
Skalkaho	3.9	3.0–4.9 (6)	Schladweiler 1968, this study
West Fork, MT	3.2	2.9–3.6 (3)	Schladweiler 1968
Liberty	3.5	3.1–4.4 (3)	Weber 1975
Green Mt.	3.2	2.5–3.7 (4)	Hoffman 1981
Eiby Creek	4.0	3.4–5.0 (4)	Hoffman 1981
Duck Creek	2.7 (1)		This study
Hudson Bay Mt.	2.6 (1)		This study

[a] Calculated from annual means. Annual means are based on samples ≥10 counts only, if *n* values are known.

[b] Years of data are in parentheses.

[c] No *n* values or ranges presented.

[d] No *n* values or annual data presented.

Hardwicke Island (Table 18.19) [50a–c]. In general, mean late-summer brood size tends to be smaller in coastal than interior populations (Table 18.21). This is partly a result of larger clutch sizes of interior birds but could also indicate a higher summer mortality among coastal chicks (see 18.4.3).

18.5.3 Is brood size related to the proportion of hens with brood?

Data from Comox Burn and Hardwicke Island suggest there are variations in the percentages of females that produce broods among years and in the mean numbers of chicks produced to late-summer by successful hens. Are years with small broods also years with few broods? We examined this question by plotting mean brood size, by year, against the percentage of banded hens known to have produced a brood within those years. There was a tendency for few broods to be correlated with small brood size at Comox Burn (Fig. 18.5), but the correlation was not significant [51a]. The same analysis for the declining population at Hardwicke Island (Fig. 18.5) showed a strong positive relationship between brood size and the percentage of hens with brood [51b]. These data suggest that years of high and low success at producing a brood are correlated with years of good and poor summer survival of chicks, though only weakly at Comox Burn. Other factors that might affect summer survival of chicks may also be involved.

18.5.4 Lifetime reproductive success

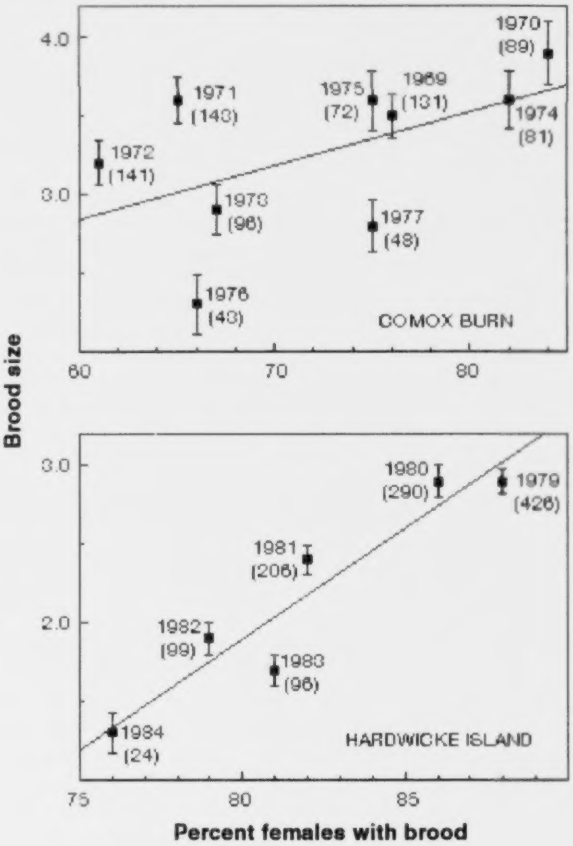
(a) *Males*. Males are promiscuous, their territories are dispersed, there is strong circumstantial evidence that some breed more than others (McNicholl 1978; Lewis and Zwickel 1981; Hervieux et al. 1993), and copulation is rarely observed. These factors make it difficult, if not impossible, to determine the reproductive success of individuals. About all that can be suggested is that since sex ratios of adults are usually balanced, average lifetime reproductive success of males is likely similar to that of females, perhaps greater in populations where female mortality exceeds that of males.

Virtually all adult males take territories (Bendell 1954; Lewis and Zwickel 1980; Lewis 1984*b*) and presumably attempt to breed, but two factors contribute to considerable variation among individuals: (1) differences in life span, and (2) a polygynous mating system with skewed breeding among individuals (Hervieux et al. 1993). Because of problems in determining individual success, we have no measure of this variation.

(b) *Females*. Lifetime reproductive success of females can be estimated more easily than for males, since they, as with males, have a relatively high fidelity to breeding areas (Jamieson and Zwickel 1983*a*; and see 17.2.2(d)), and because (1) their offspring accompany them for several weeks following hatch and (2) in some populations at least, females with brood are relatively tame and, if banded, easily identified from unique band combinations.

We estimated lifetime reproductive success (number of young produced to late summer) of 110 females banded as yearlings for three annual cohorts at Comox Burn$_{cp}$.[30] Among these hens, 22% were never seen with brood. Among those known to have produced broods (n = 86), 66% produced one, 23% two, 7% three, 1% four, 1% five, and 1% six. Among all hen years,[31] these birds produced 175 broods (130 known, 45 estimated for birds known to be alive but not seen in some years), a mean of 1.6/hen.[27] They raised 165 broods to late summer (123 known, 42 estimated for birds known to be alive but not seen in some years), a mean of 1.5/hen. Fifty-seven percent (n = 63) are known to have produced a brood as yearlings, and 59% (n = 65) were seen with broods as adults. Among 88 adult hen years, 76% (n = 67) were classified as with brood, significantly more than for yearlings [52].

Fig. 18.5. Females with brood (in %) as related to mean brood size (±SE) by year, Comox Burn and Hardwicke Island. Annual sample sizes for broods are in parentheses.



Birds in our sample produced an estimated 570 chicks to late summer throughout their lifetimes, a mean of 5.2/hen[32] (Table 18.22). In its broadest sense, however, reproductive success is not fulfilled until one's offspring contribute to breeding, which is dependent on their over-winter survival and subsequent recruitment as breeders (Fitzpatrick and Woolfenden 1988).

18.6 Synthesis

Our consideration of demography has been primarily descriptive, and we have not attempted to consider mecha-

Table 18.22. Estimated number of chicks produced to late summer throughout their lifetimes by 110 hens banded as yearlings at Comox Burn$_{cp}$ in 1969–1971.

Hen classification	Brood hen years	No. of chicks
With chicks ≥14 days of age	80	282
With chicks <14 days of age	19	47
With chicks, age unknown	31	102
Hens known alive, not seen	45	139
Total	175	570
Mean number of chicks produced per hen:		
	570/110 = **5.2**[a] (0–19[b])	

[a] Estimate considered minimal because (1) some lone hens were seen only once, sometimes before nesting, and some of those likely moved off the study area to nest and (2) number of broods <14 days of age were reduced by 28% (Sopuck 1979), although some were >10 days of age and past the period of high summer mortality.

[b] Hen estimated to have produced 19 chicks was not seen in 2 of 8 years, so this estimate is minimal. She had chicks every year seen.

nisms of population control, the principal objective of a future publication. Despite this, some points are suggestive, and we allude to them here in anticipation of a more thorough consideration in our later work.

Beginning in 1950, there have been a number of relatively long-term, intensive population studies of blue grouse in various parts of their range, i.e., ≥5 years in length. The most long-term and intensive have been in coastal British Columbia, and we lean heavily on these. Nevertheless, comparisons with data from other studies, especially for interior races of blue grouse, allow us to examine our results for their generality.

Breeding densities can vary markedly, both temporally within areas, and among areas. Reported densities vary from very low to some of the highest recorded for any tetraonine, perhaps *the highest* in terms of biomass (Zwickel and Bendell 1985). In general, coastal populations in early successional forest show the greatest changes and most extreme densities. Interior populations, usually occupying more stable habitats, tend to vary less and occur at more moderate densities. Densities in subalpine populations and at the northern and southern extremes of distribution are relatively sparse.

Most blue grouse spend the majority of each year away from breeding range. Here, they may be spread over large areas compared to those on breeding range and over extensive areas—density appears sparse.

Interpreting sex ratios of yearlings on breeding range can be difficult because of differences in the behaviour and vulnerability to capture of males and females. Although there are exceptions, most evidence suggests sex ratios of blue grouse are balanced throughout the life of a population.

If one makes certain assumptions, age structure can provide an index of turnover or replacement in a population. Data from a number of studies indicate numbers of yearling females were usually adequate, or more than adequate, for replacement of adults that die, even though the proportion of yearling females on breeding range varies among years.

By autumn only two age classes can be identified with certainty, adult and juvenile. Hunting samples from this season show variation among years in percent juveniles in the kill. Those from coastal and interior subspecies suggest, on average, about 50% and 60% of the autumn population is composed of juveniles, respectively. This same coast–interior tendency is apparent among autumn-collected museum specimens.

Beyond 1 year of age, annual survival appears constant among all year classes on most coastal British Columbia study areas, averaging about 75% and 70% for males and females, respectively. That of females, however, may be lowered by heavy hunting pressure where that occurs, e.g., at Comox Burn in later years of study. Annual survival of adult males in an interior population in western Montana was approximately 70%. These data suggest a high annual survival for adults. Boag (1966), reported lower survival for males and females in a declining population in Alberta.

Blue grouse are among the most long-lived of all grouse. The second greatest longevity documented for any tetraonine in the wild was an interior male blue grouse ≥14 years of age. The oldest coastal males ($n = 2$) were 12 years of age when last seen, the oldest female, 11.

First-year survival is difficult to evaluate, for it is confounded by dispersal. Some data indicate chick losses are relatively heavy in the first 2–4 weeks following hatch, with a relatively small loss over the remainder of the summer. Summer losses vary annually within and among areas, with late-summer brood sizes generally lower in coastal than interior populations. Indirect estimates of winter survival of juveniles on Vancouver Island range from 41% to 54%. Similar estimates for two populations in western Colorado were 38% and 48%.

Among chicks marked at 1 day to >10 weeks of age at Comox Burn and Hardwicke Island, 14% survived to at least 1 year of age, with no difference between areas. At least 40% of all chicks banded at ≥11 weeks of age at Comox Burn, and 37% of those at Hardwicke Island, lived to at least 1 year of age.

The percentage of banded females that produced broods at Comox Burn and Hardwicke Island was less in yearlings than adults. That of adults was usually in the range of 80%–90%. Annual differences within areas appear to be principally a result of variations among yearlings.

Mean late-summer brood sizes of yearling females tend to be smaller than those of adults, but not significantly so. Thus, unless yearlings have a greater total brood loss, they are as successful at raising chicks as adults. In general, late-summer brood sizes of interior grouse are larger than those of coastal birds, but perhaps no more so than can be explained by differences in size of clutch. Our data suggest mean late-summer brood size is positively correlated with the percentage of hens known to have produced broods within years.

We have not been able to estimate lifetime reproductive success of males because of their polygynous mating system and skewed breeding among individuals. Among 110 hens banded as juveniles or yearlings (in three cohorts and monitored for ≥8 years), 78% produced at least one brood during their lifetimes. These hens produced an estimated 570 chicks to late summer, 5.2/hen over their lifetimes. This is likely more than adequate for replacement.

Endnotes [Chapter 18]

1. In most studies cited in Table 18.1, a high proportion of males were colour-banded, territories were counted, and census plots were relatively large. This increases the reliability of estimates, for banded individuals can be counted directly and the ratio of edge to total area is reduced as size of area is increased, which decreases errors in tallying birds along borders.

2. Another possible exception involves reported densities of 30–56 territorial males/km^2 at Centennial Ridge, WY (Harju 1974). We excluded this estimate because it is not clear the calculation is comparable to other estimates.

3. At Middle Quinsam and Comox Burn, reported densities were virtually identical to those determined by our more intense censuses in 1976.

4. We excluded estimates of 4–39 females/km^2 for southeastern Wyoming (Harju 1974) because the method of computation does not appear comparable to other estimates.

5. In contrast, Cade (1985) found males and females in the same flocks, but provided no estimates of winter density or ages of birds seen.

6. This is especially important in blue grouse because of their migratory and sex specific behaviour. For example, in early spring, displaying males are most conspicuous and nesting females secretive—the observed sex ratio favours males. By mid to late June, many males are leaving breeding areas and hens with broods are most obvious—the sex ratio increasingly favours females through the rest of the summer (Fowle 1960).

7. Nalbandov (1976) suggested that the primary sex ratio is mainly a theoretical concept because of difficulties in determining sex of zygotes, but recent advances in molecular genetics likely alleviates this problem. There are no such data for blue grouse at this time.

8. Sex was determined internally for chicks that died before external characteristics were apparent.

9. Sex can be determined by plumage after ~6 weeks of age (Caswell 1954*a*; Nietfield and Zwickel 1983).

10. Data from Vancouver Island were collected on opening weekends of grouse seasons, the last weekend of August or first weekend of September—most juveniles would have been from 7 to 11 weeks of age. At Chumstick, Conconully, and Eight Mile Creek, samples were collected on the second weekend in September to the first weekend of October, and most chicks would have been ~13–18 weeks of age. At Middle Park samples were collected from the second weekend in September to the second weekend in October, and since peak hatch is about 1 month later than in northcentral Washington, most chicks would have been ~9–14 weeks old.

11. Hunters may be selective in birds they shoot, perhaps choosing larger, smaller, or distinctively coloured birds from those available. As well, availability of young males and females might vary should the sexes differ in areas, or habitats, to which they migrate (the fall phase of dispersal). Migration of young mainly begins in early September on Vancouver Island but was likely well underway by the time collections were made in northcentral Washington and Middle Park.

12. Postnuptial moult begins on lowland Vancouver Island as early as 13 May in males, 31 May in broodless females, and 14 June in brood females (Zwickel and Dake 1977). Moult is underway in all yearling males within ~1 week of the first bird to moult, that of yearling females within ~5 weeks of the first, within the classes broodless and brood, respectively. In some populations, primary moult of some yearling males and females appears to be completed by ~1 September, and these birds cannot be separated from adults.

13. Presumably the behaviour of yearling males and females is most comparable during this period, and the non-breeding status and secretiveness of males is countered at least in part by reduced observability of incubating females.

14. Another factor that could be involved is a difference in vulnerability of males and females to hunters. For example, brood hens may be more vulnerable than males because of differences in behaviour or because they are in family groups while many males are alone, or at most, usually occur as twos and threes at this season.

15. Banding samples are potentially biased by catchability of males and females, by techniques used, and by effort expended in working with the two sexes. For example, in populations in which individuals are relatively tame, 75%–80% of adult males and females may be captured and marked. But in some populations individuals are relatively wild and few, or no, males are catchable, while many hens, once with brood, can be caught. There are different degrees of catchability of males and females between these extremes. Hunting samples of adults have all the potential biases associated with the examination of sex ratios in yearlings.

16. An average of ~80% of adult males and ~75% of adult females were individually marked each year.

17. A deficiency of adult females at Comox Burn$_{CP}$ appears related to heavy hunting pressure on this segment of that population (Zwickel et al. 1983).

18. Some of the variation among areas is dependent on when samples were collected, as the proportion of yearlings identified may change between spring and summer. Data represent all samples from breeding range.

19. Ninety seven percent (470/487) were taken after 31 March, i.e., during breeding season.

20. Numbers of adult plus yearling males were adjusted to equal those of adult plus yearling females (see Zwickel et al. 1975). This weighting assumes a balanced sex ratio among adults, which appears true in most populations.

21. To minimize problems associated with differential availability, we weighted yearlings and adults as with samples from hunters.

22. For statistical analyses, males in age classes 7–11, and females in age classes 6 and 7, were combined because of small samples.

23. For statistical analyses, males and females in age classes 4 and 5 were combined because of small samples.

24. Annual survivals calculated by us from data in Redfield's (1975) Tables 8 and 9. Redfield also presented "adjusted" mortality data for females that indicate survivals of 55% for each age class, respectively.

25. All birds identified as yearlings on our main study areas at Comox Burn and Hardwicke Island were used for analyses of survival of yearlings to age 2. To be included in analyses of adult survival a bird had to be classified as a *resident* adult. Adults seen only on the study areas were considered as residents, but those seen 2 out of 3 years outside the boundary were not included, and vice versa.

26. Potential biases must be considered in estimates of production. Some banded females may be identified on an area in spring but produce a brood outside that area, or move outside soon after hatch and not be identified as a brood hen. This inflates the proportion counted as broodless. Large study areas with proportionately less edge are least subject to such bias. In contrast, most banded hens are identified when with brood, and those without young may not be identified because they are more wary, or have moved off the area soon after loss of nest or brood. Females that don't breed may be missed. These factors inflate the proportion of females considered as with brood. We have no estimates of sizes of these biases but recognize they exist. In the absence of such estimates, we assume the overall effect will be relatively small, since those that inflate the proportion of hens counted as broodless will tend to be cancelled by those that inflate the proportion counted as with brood. We assume these biases are constant among years and areas.

27. Includes all hens seen at least once with brood, not only those raising a brood to late summer.

28. For example, in the Methow Valley in 1968, 50% of all females sighted in June ($n = 168$) were with brood, 79% in July–August ($n = 115$). Numbers of brood hens seen showed little change between periods, 84 and 91, respectively. Numbers of lone hens, 84 and 24, respectively, showed a large and significant decrease [46] caused by some hens leaving breeding range early (see 17.1.4).

29. Reliable counts of very young chicks are difficult to obtain. To minimize this problem, we used only counts from late summer to estimate numbers of chicks produced per successful female. In our own studies, we used pointing dogs to help find chicks (except at Lower Quinsam), but this is not true for some studies reported by others. Even with dogs, chicks can be missed, so reported mean brood sizes are minimal. Also, in most studies, including ours, repeat counts of the same broods may occur. Ideally, a single, maximum count would be used for each brood, but this is not logistically feasible with blue grouse because some hens are not marked and, even if marked, may not always be identified.

30. Computations are based on yearling female cohorts for 1969 ($n = 35$ females), 1970 ($n = 26$), and 1971 ($n = 49$). Cohorts for 1969 and 1970 were each monitored for 9 years (the oldest hen in each was 8 years of age). The 1971 cohort was monitored for 8 years with only one hen seen in year 8. Five classes of hens were considered, four with brood and a fifth without brood (lone hens). Classes of brood hens were (1) hens with chicks ≥14 days of age (assumption: if brood survives to 14 days, it will survive to late summer), (2) hens with chicks <14 days of age (corrected for total brood losses), (3) hens for which age of chicks was not determined (corrected for broods <14 days of age and for total brood losses), (4) hens known to be alive but not seen in a given year (corrected for broods <14 days of age and for total brood losses in the latter group). Each hen was assigned the mean late-summer brood size for its respective year.

31. Includes lone hen years.

32. Figures are minimal because some hens, especially yearlings, may have produced broods away from our study areas (see footnote *a*, Table 18.22).

CHAPTER 19

Predators

Probably the commonest death for many animals is to be eaten by something else, . . .

Charles Elton (1927)

Predation is a dynamic and powerful force that can affect prey at any one or more of the individual, population, community, or evolutionary levels. As a relatively large herbivore, grouse attract a wide range of vertebrate predators, including reptiles, birds, and mammals. In this chapter, we examine the seasonal pattern of predation on blue grouse and their nests and identify the kinds of predators and their relative impacts on different sex and age classes. Impacts at the population level will be considered in a future publication.

We use three principal sources of data from Vancouver and Hardwicke islands for analyses: (1) evidence from remains of grouse or nests found in the field, (2) direct observations of attacks on grouse, and (3) evidence from the examination of droppings of mammals, or other sign. We also review information from other studies, especially from interior populations.

19.1 Predators of grouse

19.1.1 Seasonal pattern of predation on breeding range

Our most extensive sample comes from remains of grouse found in the field. We classified all kills as *recent*, <30 days since occurrence,[1] or *old*, >30 days since occurrence.[2]

(a) *Males*. Recent remains at Comox Burn and Hardwicke Island indicate that numbers of males killed by predators increased steadily through April, peaked in May, then declined rapidly (Fig. 19.1).[3] The increase in April and peak in May coincide with migration onto breeding range and the period of peak display, respectively. The decline, beginning in early June, coincides with a marked reduction in singing and display, and a more secretive behaviour of males that occurs at about this time. A large decrease in numbers of remains, beginning in late June, coincides with a further reduction in display behaviour, coupled with the beginning of migration to winter range of yearling males (Sopuck 1979) and of the abandonment of territories by adult males (Lewis 1985*b*) as they begin to abandon territories.

(b) *Females*. The temporal pattern of recent remains (Fig. 19.1) was significantly different from that of males [1]. There was a similar, but slightly later increase among females than males in April, peaking in May. Later increase reflects the later migration of females onto breeding range. The peak in May coincides with nesting and might indicate a high vulnerability of nest hens to predation. However, direct evidence from nesting hens indicates few are killed even though their nests may be destroyed (see 19.2.1). Many hen remains at this time may represent non-breeders. There was a slow, but steady, decline in kills throughout the rest of the summer. The decline, beginning in late June (Sopuck 1979), coincides with the gradual departure of unsuccessful and (or) non-breeding females to winter range.

In general, the seasonal pattern of predation on males and females is consistent with what is known about relative availability of the sexes, with availability reflecting both presence or absence on breeding range and seasonal changes in behaviour.

(c) *Juveniles*. Our samples of recent kills of juveniles are too small and potentially biased to justify a detailed analysis. Biases are introduced because many small juveniles are likely eaten whole, leaving no remains, or carried to dens, nests, or feeding sites. Of all recent kills reported (n = 23), 18 (78%) were found in August or early September, by which time most young birds are at least one-half grown. In contrast, of 23 witnessed attacks on juveniles, or cases in which predators were found with fresh carcasses of juveniles, 8 were in June, 8 in July, and 7 in August. This is probably more representative of the pattern of predation on this age group but likely underrepresents kills in June and July because of biases noted.

19.1.2 Age and sex of grouse killed

Age and sex of grouse killed by predators may indicate selection of certain classes of grouse, differential vulnerability among age and sex classes, or both. We examined these questions by comparing ages and sexes of kills to expected age and sex ratios among yearlings and adults on breeding range.

(a) *Age*. Among 224 yearlings and adults among recent and old remains at Comox Burn and Hardwicke Island, specific age was determined for 193 (Table 19.1). The percentage yearlings among males, 25% (29/116), was not significantly different from 30% [2], the expected minimum in a stable population. This is of special interest because behaviours of the age classes differ; most adults hold territories on which they display, most yearlings do not and tend to be secretive (see 15.2.2(b) and 15.2.2(c)).

Fig. 19.1. Approximate times of death of predator-killed grouse on breeding range, by half-month intervals. Data from Comox Burn and Hardwicke Island combined.

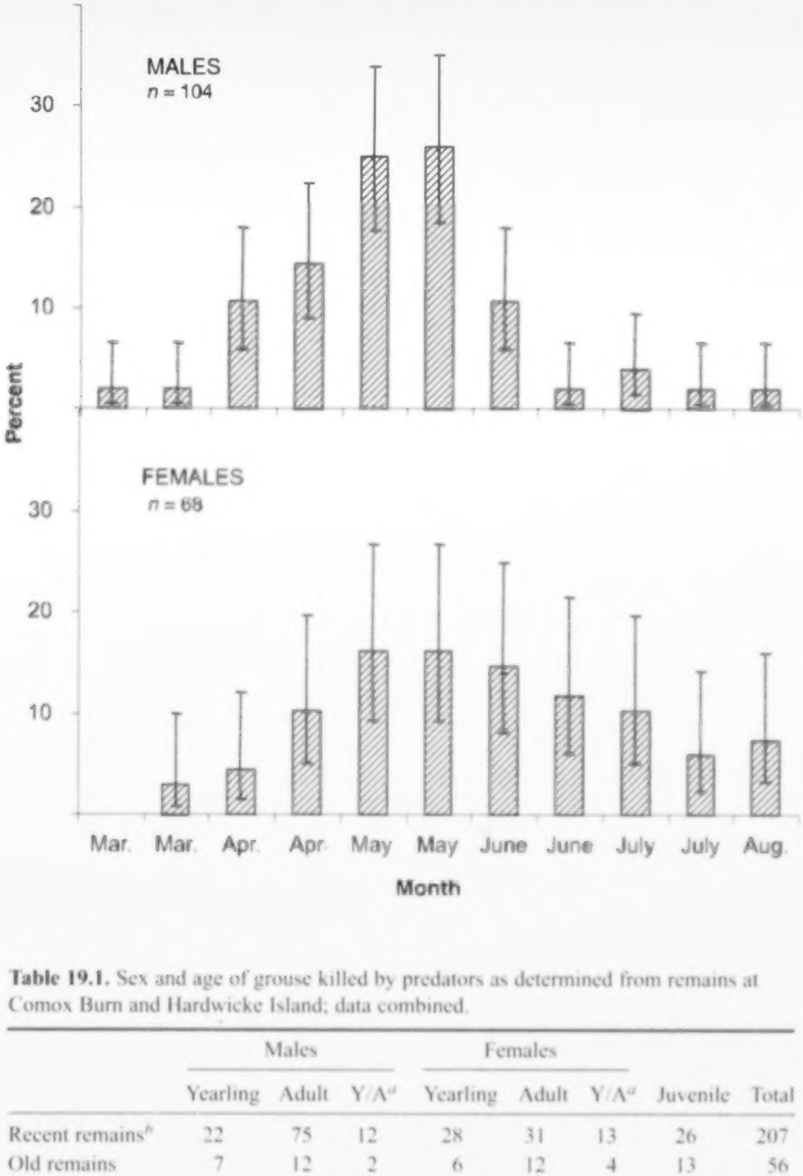


Table 19.1. Sex and age of grouse killed by predators as determined from remains at Comox Burn and Hardwicke Island; data combined.

	Males			Females				
	Yearling	Adult	Y/A[a]	Yearling	Adult	Y/A[a]	Juvenile	Total
Recent remains[b]	22	75	12	28	31	13	26	207
Old remains	7	12	2	6	12	4	13	56
All remains	29	87	14	34	43	17	39	263

[a] Yearling or adult, specific age not determined.

[b] Includes 12 cases in which predator was found with a fresh kill.

The percentage yearlings among females has usually varied between ~30% and 40% in local populations in this region. The percentage yearlings in prey remains (44%, 34/77) was significantly greater than 30% [3a] but not different than 40% [3b]. These data do not suggest any strong, differential vulnerability to, or selection by, predators, of yearlings or adults. As noted above, juveniles (39/263) are likely underrepresented in prey remains.

(b) *Sex.* Most populations of blue grouse for which information is available have had a balanced sex ratio in yearlings and adults, although an exception was the population at Hardwicke Island when at its peak and at which time females outnumbered males (Zwickel et al. 1988). The ratio of males to females among yearling prey remains, 29:34 (Table 19.1), did not differ from an expected ratio of 1:1 [4a].[4] However, among adults, there were many more males than expected, 87:43, when compared to 1:1 [4b]. These data suggest a greater vulnerability to, or selection by, predators of adult males than adult females, especially since data from Comox Burn and Hardwicke Island are combined (more females than males at Hardwicke). They also are consistent with remains of 15 blue grouse examined at a fox den in spring at Lower Quinsam, among which 12 were adult males and 3 adult females (Bendell 1955*c*).

19.1.3 Kinds of predators

Virtually all carnivorous mammals and raptorial birds that occur within the range of blue grouse can be considered as potential predators on them during some stage in their life cycle. As well, some corvids (Corvidae), rodents (Rodentia), and reptiles (Reptilia) may prey on eggs or small chicks, though, except for corvids, this is speculative.

(a) *Evidence from recent remains.* Criteria discussed by Einarsen (1956), Jenkins et al. (1964), and Dumke and Pils (1973), were used to classify 174 recent remains as evidence of kills by either birds or mammals.[5] Percentages of yearlings and adults killed by birds or mammals at Comox Burn did not differ from those at Hardwicke Island [5], so these data were combined (Table 19.2). Percentages were similar in males and females when age classes were combined [6]. Data for sexes combined indicate that 76% (116/155) of all yearlings and adults found dead were killed by raptors. In contrast, only 35% of juvenile remains suggested raptor kills, significantly lower than in yearlings and adults [7]. We suspect data for juveniles are strongly biased toward mammals, however, because raptors may take many smaller juveniles to nests or feeding sites, leaving little or no evidence behind.

(b) *Evidence from old remains.* We found 111 old remains at Comox Burn and Hardwicke Island but could classify only 25 to age or sex. Nine yearlings–adults (41%) were classified as kills by raptors, 13 (59%), by mammals. The high proportion classified as mammalian may reflect scavenging of avian kills by mammals in these older remains. Of three juvenile remnants, two were classified as avian kills, one as mammalian.

(c) *Evidence from non-lethal attacks.* One occasionally finds scattered feathers indicating a grouse had been struck by a predator, but with insufficient evidence to conclude the bird was killed,[6] i.e., the bird may have escaped. In 45 recent cases, 76% involved yearling and adult males, the remainder, yearling and adult females. These were distributed through the season approximately as were actual kills (Fig. 19.1). The large number of males suggests they may more often escape from predators after being struck than do females. In support of this contention, fewer males than females (nearly significant [8]) that were struck resulted in known kills (Table 19.3). The larger body size of males may reduce their vulnerability.

Table 19.2. Grouse killed by birds or by mammals (in %) as determined from *recent* remains at Comox Burn and Hardwicke Island (data combined[a]). Sample sizes are in parentheses.

	Birds[b]	Mammals
Yearling and adult males (93)	77	23
Yearling and adult females (62)	73	27
Subtotal (155)	75	25
Juveniles (20)	35	65

[a] 19 cases in which class of predator was not determined are excluded.
[b] All by raptors.

Table 19.3. Recent remains of grouse (in %) classified as predator kills or as "outcome of attack uncertain" at Comox Burn and Hardwicke Island (data combined). Sample sizes are in parentheses.

	Outcome	
	Kills	Uncertain[a]
Yearling and adult males (138)	75	25
Yearling and adult females (79)	86	14
Grand total (217)	79	21

[a] Attacks in which there was clear predator–prey contact but insufficient evidence to conclude the grouse was killed.

(d) *Evidence from direct observations.* Ideally, the least biased method of identifying what species prey on grouse would be to make direct observations of attacks. However, these opportunities occur rarely and tend to be strongly biased toward observations of avian attacks because of the secretive nature and nocturnal behaviour of many mammalian predators. Such attacks are also biased toward situations in which the observer has placed the bird at risk by flushing it, or otherwise distracting it from its normal routine.

Of 49 witnessed attacks at Comox Burn, Hardwicke Island, and subalpine Vancouver Island, 82% were classified as "observer induced", i.e., observers may have put the birds at risk (Table 19.4). Induced attacks were significantly less successful than those that were not [9]. Induced attacks are opportunistic, and their lower success rate may reflect a lack of readiness on the part of the predator to take advantage of the opportunity. Among all species, accipiters (Accipitridae) were the principal predators, with goshawks accounting for 75% (15/20) of all witnessed kills. All attacks but one on adults or yearlings were by goshawks, and all kills by smaller raptors were of juveniles. Witnessed kills included one adult male, one adult female, and 18 juveniles.

Only a few attacks by non-raptors have been observed (Table 19.4). In one case a raven swooped at a brood hen on a stump, with the hen jumping to the ground and the raven flying off. This was likely not a serious predation attempt.[7] In a second case a black bear pursued a brood hen as she appeared to try and lead it from the area (Sullivan 1979). Termination of the attack was interrupted by the observer. A wolf (*Canis lupus*)–grouse confrontation may, or may not, have involved an attack by the wolf. In this case, the observer was preparing notes after handling chicks at a nest when he heard the hen clucking loudly. She was flying at a large wolf in typical brood defence behaviour. The wolf may have followed the observer to the nest and was driven away by him.

In a few instances predators have been found with fresh kills, but the attack was not witnessed. Ten of 11 such cases at Comox Burn and Hardwicke Island involved goshawks (2 were likely observer induced), and 1, a red fox (*Vulpes fulva*). See also 15.1.4 for other behavioural reactions of grouse to interactions with predators.

Table 19.4. Observed attacks on blue grouse on Vancouver and Hardwicke islands (data combined[a]).

	No. of attacks		
Species of predator	Observer-induced[b]	Not induced	Total
Northern goshawk	25 (11)	4 (4)	29 (15)
Cooper's hawk	1 (0)	1 (1)	2 (1)
Sharp-shinned hawk[c]	1 (1)	0	1 (1)
Merlin[d]	1 (0)	2 (2)	3 (2)
Merlin or sharp-shinned hawk	1 (1)	0	1 (1)
Northern harrier	1 (0)	1 (0)	2 (0)
Bald or golden eagle	3 (0)	1 (0)	4 (0)
Kestrel[e]	2 (0)	0	2 (0)
Raven	1 (0)	0	1 (0)
Unidentified raptor	2 (0)	0	2 (0)
Black bear[f]	1 (0)	0	1 (0)
Wolf	1 (0)	0	1 (0)
Total	40 (13)	9 (7)	49 (20)
Percent successful	33%	78%	41%
Percent of total	82%	18%	

Note: Numbers of successful attacks are in parentheses. One unidentified raptor and two goshawk attacks at Hardwicke Island and for which the outcome was not known are excluded.

[a] Includes two goshawk attacks in the subalpine from King (1971) and one goshawk and one bald eagle attack at Middle Quinsam. All others are from Comox Burn and Hardwicke Island.

[b] Observer may have placed the bird at risk by flushing or distracting it.

[c] *Accipiter striatus*.

[d] *Falco columbarius*.

[e] *Falco sparverius*.

[f] *Ursus americanus*.

(e) *Evidence from droppings of mammals and other sign.* Remains of prey found in mammal droppings or other sign sometimes can be used to identify predators to genus or species. Although one cannot be certain whether the prey was killed or scavenged, such information can be suggestive.

At Comox Burn, great horned owl (*Bubo virginianus*) feathers were found at two raptor kills. Leg bands were recovered from each of one black bear dropping (Sullivan 1979) and one presumed mountain lion (*Felis concolor*) dropping (Forbidden Plateau area, ~7.5 km from Comox Burn, by RM Masters, pers. comm.). Two radio transmitters were found inside logs where they could have been taken only by mammals not larger than a pine marten (*Martes americana*). And one coloured leg band and two left wings were found at a red fox den.

Wolves were common and their droppings abundant at Hardwicke Island. They are the only large carnivore regularly found there, although transient black bears and mountain lions have been recorded—one mountain lion and no bears during our studies. That wolves may occasionally kill blue grouse is indicated by two radio transmitters bitten by large mammals, four single or sets of bands chewed by large mammals, and leg bands found in four wolf droppings. Two radio transmitters were found at roost sites of bald eagles on this island.

(f) *Evidence from other studies.* There are few identifications of predators of blue grouse in the published literature other than occasional anecdotal notes, e.g., Bent (1932), Jewett et al. (1953), and Craighead and Craighead (1956). Some have been noted in unpublished theses, however. King (1971) saw an unsuccessful attack by a goshawk on a male on Vancouver Island. In northcentral Washington, Henderson (1960) came upon a golden eagle eating a female, but hesitated to conclude the grouse was killed by this bird. Caswell (1954*b*) found direct or indirect evidence of kills by golden eagles, great horned owls, and goshawks in westcentral Idaho. He encountered five goshawks with kills and considered them the main predator of grouse in his area. He noted that many grouse escaped attacks by this raptor. Pekins (1988), in northcentral Utah, found the remains of a male killed in winter, presumably by a bobcat (*Lynx rufus*).

At Sheep River, Boag (1964) found blue grouse remains at the entrance of a coyote (*Canis latrans*) den, and reported an instance of lynx (*Lynx canadensis*) predation. He thought the major predator there was the golden eagle, for grouse remains at an eyrie represented 9%, 15%, and 17% of all items found in each of 3 years for which data were available. Blue grouse accounted for 15% of the biomass of prey remains at this eyrie (Boag 1977).

In southeast Wyoming, Harju (1974) saw prairie falcons (*Falco mexicanus*) kill males and young. He recorded three kills of adult males, one by a great horned owl and two by red-tailed hawks. He thought coyotes were a major predator of grouse there, but presented no evidence for this contention. Weasels (*Mustela* spp.) and badgers (*Taxidea taxus*) also were suggested as significant predators, but no evidence was presented.

We have found remains of 50 blue grouse presumed to have been killed by predators in our studies of interior populations. Evidence was adequate to identify 34 to sex and age (only age for juveniles) and to classify the likely predator (Table 19.5). As at Comox Burn and Hardwicke Island, most yearlings and adults were killed by raptors and proportionally more juveniles by mammals, a significant difference between the two groups [10]. An eagle, likely golden, three red-tailed hawks, and a coyote were implicated in kills, each in one attack.

Four attacks by raptors have been observed by us in interior populations. Only one, by a goshawk and observer induced, may have been successful. Others were by red-tailed hawks ($n = 2$), both observer induced, and a marsh hawk, not so induced. In a fifth case, an adult redtail was flushed from a bunchgrass hillside with a freshly killed carcass of a banded

Table 19.5. Numbers of grouse killed by birds or by mammals as determined from remains of interior birds.

	Birds[a]	Mammals
Yearling and adult males	8	2
Yearling and adult females	11	1
Subtotal	19	3
Juveniles	6	6

Note: Data from the Methow Valley, Duck Creek, Skalkaho, and Hudson Bay Mt. Sixteen cases in which class of predator or age or sex of prey was not determined are excluded.

[a] All kills by raptors.

juvenile. The hawk had trouble gaining elevation and dropped the carcass (205 g body mass) when shouted at.

(g) *Autumn and winter.* In these seasons, when blue grouse spend much of their time in trees, one might expect the impact of mammalian predation to decline. Indeed, this appears true, for Hines (1986*a*) reports that 44 of 74 radio-marked juveniles killed in autumn or winter on Hardwicke Island were taken by raptors. Only three were classified as mammalian kills, and the predator could not be identified in the remainder. Thus, of those that could be classified, 94% (44/47) were thought to have been killed by raptors, significantly greater than among yearlings and adults on breeding range, 76%, as indicated by recent remains (19.1.3(a)) [11]. This contrasts sharply with the spring–summer season when smaller juveniles spend most of their time on the ground and appear most vulnerable to mammals. Only Hines has presented much data on winter predation.

19.2 Predators of nests and nest hens

19.2.1 Kinds of predators

All identifications of predators that may have destroyed nests are circumstantial and based on evidence, or lack of it, at the site, for none has been found at a nest. Avian predation on nests was mainly by corvids: jays or ravens. The only common corvids at Comox Burn and Hardwicke Island were ravens (*Corvus corax*), with Steller's jays (*Cyanocitta stelleri*) uncommon. We used generally accepted criteria, in conjunction with other evidence found at the sites, e.g., feather and carcass remnants, to identify predators that destroyed nests.[8] Nests also may be terminated by killing the hen when away from the nest.

Of 123 nests terminated by predators at Comox Burn and Hardwicke Island, 35 were classified as to kind of predator (Table 19.6). Of these, 83% were destroyed by mammals,[9] clearly the most important agent of destruction. Mammals killed two hens away from nests—the eggs were intact—and two at nests. In the latter cases, all eggs disappeared from one nest and in the other, four of six were eaten by a corvid. In the only case involving a raptor, the female was killed at the nest and the eggs were undisturbed. In 13 cases with evidence at the nest, e.g., eggs or eggshells ($n = 10$) or female feathers suggesting she had been struck or flushed wildly, the predator could not be identified. The most common situation at predator-terminated nests was a disappearance of all eggs, with no evidence beyond an empty nest.

Disappearance of all eggs with no evidence is puzzling. We suspect many of these clutches were taken by black bears at Comox Burn because Prach (1976) found shell fragments from grouse-sized eggs in 18 of 112 bear droppings from this area.[10] These droppings were collected throughout spring and summer, in which period nests are commonly available for only 5–6 weeks, so bears may have been an important agent of nest destruction there. All eggs disappeared, with no other evidence, in 61% of all destroyed nests at Comox Burn and Hardwicke Island, but there were no bears at Hardwicke. Wolves were relatively common at Hardwicke and may have been responsible for some of the loss there. Other resident species on our study areas that might have caused this type of predation include ravens (common), Steller's jays (uncommon), red squirrels (*Tamiasciurus hudsonicus*, uncommon), weasels (rare), pine marten (rare, Comox Burn only), and raccoon (*Procyon lotor*, very rare, Comox Burn only).

Table 19.6. Numbers of nests destroyed or terminated by different classes of predators at Comox Burn and Hardwicke Island (data combined), as related to stage of nesting cycle.

	Stage of nesting cycle			
Predator	Laying	Incubation	?	Percent
Corvid	2	2	1	4
Raptor	0	1	0	<1
Mammal	3	21	5	24
Evidence unclear[a]	1	6	6	11
No evidence[b]	6	63	6	61
Percent (n = 123 nests)	10	75	15	

[a] Some evidence at nest but insufficient to identify the predator.

[b] All eggs disappear and no evidence with which to identify the predator.

A common sign at some nests attributed to destruction by mammals was a line of feathers leading from the nest and extending out as far as several metres. Numbers and kinds of feathers indicated the hens were struck by small mammals (e.g., squirrels, weasels, or pine martens) while on the nest, but that they escaped. Among 68 banded hens whose nests were destroyed, 14 appear to have been struck (Table 19.7), 12 at the nest. Seventy-four percent do not appear to have been struck, and 56 (82%) are known to have survived following loss of their eggs.

19.2.2 Partial predation on nests

In some cases, predators may take only some eggs and the nest then be deserted. In nine such cases, all at Comox Burn, two nests lost one egg, two lost three, three lost four, one lost five, and one lost six. Thus, seven of nine lost >2 eggs. In other instances, the hen may continue to incubate and produce a successful hatch. At Comox Burn and Hardwicke Island (data combined), 8% of all successful nests lost ≥1 egg (20/264); 13 lost 1, 6 lost 2, and 1 lost 3. There is thus a tendency for hens who lose eggs to continue to incubate. Among 29 nests suffering partial predation, only two instances occurred during laying and both clutches were deserted. Clutches losing ≥2 eggs may lose them one at a time, over a period of days, or all at once. Partial predation was most likely caused by ravens (common), weasels or pine marten (both rare), or perhaps, red squirrel (uncommon on both study areas).

Partial predation makes clutch sizes conservative as reported in 10.6.2. The effect is small, however, since only 1.4% of 1035 eggs disappeared or were destroyed in successful nests at Comox Burn and 1.7% of 770 eggs at Hardwicke Island. In support of this conclusion, mean numbers of postovulatory follicles of yearlings and adults at Comox Burn did not differ from mean clutch sizes there (Hannon 1981).

Table 19.7. Fates of banded females whose nests were terminated by predators at Comox Burn and Hardwicke Island (data combined).

	Fate of female[a]			
	Alive	Dead	?	Percent
Female struck	6	5[b]	3	21
Female not struck[c]	47	0	3	74
Unknown	3	0	1	6
Percent (n = 68 females)	82	7	10	

[a] Following destruction of clutch.
[b] Two were killed away from nest.
[c] No evidence at the nest of female having been contacted by the predator.

19.2.3 Stage at which nests are destroyed—laying or incubation?

Nests may be terminated by predators at any time after the first egg is laid. We used the Mayfield (1961) method to examine for differences in the loss of nests during these two stages of the nesting cycle. We used data from 120 nests at Comox Burn and 107 from Hardwicke Island for this analysis (Table 19.8).[11] There was no significant difference in stage of loss at either area [12a, b], but which may reflect the small samples for the laying period.

We also compared nest success for these two periods between Comox Burn and Hardwicke Island. Success did not differ during laying [13a] but was significantly lower at Comox Burn than at Hardwicke during incubation [13b]. We think higher losses at Comox Burn reflect a greater diversity, and apparent densities, of mammalian predators there than at Hardwicke. A difference during incubation, but not laying, may indicate mammals are cueing in on incubating hens (by scent), as reported for greater prairie-chickens (Bowen and Simon 1990). We found few active nests prior to working with pointing dogs which find most nests by scent.

19.2.4 Effects of nesting cover

We described and made sketches of nearly all nest sites at Comox Burn, and all were rated as having *poor*, *moderate*, or *good cover*.[12]

Cover at nests of yearling and adult hens (Table 19.9) did not differ significantly between age classes [14]. Sixty-four percent of all females selected sites classified as good, 89% as good or moderate.

Although females tended to select nest sites with good concealment, there was no difference in the success of females with nests in the different cover ratings (Table 19.10) [15]. Failure to detect a difference may result in part from the small sample of nests classified as poor. Nevertheless, "quality" of cover based on our criteria does not offer a clear explanation for failure of some nests because of predation. Sopuck (1979), working with 57 radio-marked females at Comox Burn, also reported that age of hen and nesting success were independent of nesting cover. Since most nests are destroyed by mammals, which often hunt at night and by scent, amount of cover may not have a great influence on success. Nest site selection may be related in part to factors other than security from predators, e.g., to modify the immediate environment of the eggs or hen.

Table 19.8. Nest loss (%) at Comox Burn and Hardwicke Island during the laying and incubation periods as determined by the Mayfield Method (1961).

	Laying	Incubation	Lay and incubation
Comox Burn (1969–1977)	7 (98)	52 (1372)	55 (1470)
Hardwicke Island (1979–1984)	0 (45)	21 (1307)	21 (1352)

Note: Numbers of nest days are in parentheses. Numbers of nests contributing nest days: Comox Burn, $n_{\text{lay}} = 18$, $n_{\text{inc}} = 119$; Hardwicke Island, $n_{\text{lay}} = 17$, $n_{\text{inc}} = 90$. Includes nests of adult, yearling, and unknown age females.

Table 19.9. Quality of nesting cover (in %) by age of hen at Comox Burn (data for 1962–1965 and 1969–1977 combined).

	Nesting cover			
	Poor	Moderate	Good	n
Yearling females	4	35	61	23
Adult females	9	25	66	65
Female age unknown	16	21	62	61
Total	11	25	64	149

Table 19.10. Success or failure of nests (in %) as related to quality of cover at Comox Burn.

	Nesting cover		
	Poor	Moderate	Good
Successful hatch	41	62	62
Nest lost to predator	59	38	38
n	17	37	95

Note: Data for 1962–1965 and 1969–1977 combined.

19.2.5 Predation on nests—interior populations

Little information is available on nest predators of blue grouse in interior populations. We have accumulated data on only 18 interior nests terminated by predation (12 in the Methow Valley). Two were terminated by corvids, three by raptors, six by mammals, four by unknown predators, and in three cases there was no evidence with which to identify the predator. In cases in which the predator could be identified, mammals were most important. These data indicate mammals may terminate fewer nests here, in a relative sense, than in coastal areas, but in view of the small sample, this may not be meaningful. Neither of two banded hens whose nests were destroyed were killed.

19.3 Synthesis

Within sexes, yearling and adult blue grouse on breeding range appear to be killed by predators in approximate proportion to numbers present at any given period, but with vulnerability also influenced by seasonal behaviour. Vulnerability appears to be determined by both absence or presence on breeding range and changes, or differences, in behaviour among various classes of birds.

Evidence from recent remains of yearlings and adults and from witnessed attacks indicate that raptors, especially accipiters, are principal predators of these birds. In contrast, recent remains indicate mammals are the main predators of juveniles on breeding range, but these data are subject to bias. Raptors appear to be the principal predators in autumn and winter.

More adult males than adult females than expected on the basis of their relative abundances are killed on breeding range. This may reflect behavioural differences between the sexes. A number of different birds and mammals have been identified as predators of blue grouse on breeding range, with raptors, especially goshawks (where they occur), most important.

In contrast to predation on birds themselves, eggs of blue grouse are most often taken by mammals, with raptors and corvids relatively unimportant. There is little indication that nesting cover influences nest success and the heavy destruction by mammals may be because they often use scent when hunting. That nests are more likely to be terminated during incubation, when the hen is on the nest most of the time, rather than during laying, is consistent with this view. Evidence from banded birds indicates females whose nests are destroyed usually escape even though they may have been struck by the predator.

Endnotes [Chapter 19]

1. Recent remains were often clearly fresh. They usually could be separated from old remains by presence or absence of blood, degree of dehydration, or degree of weathering, the latter involving matting of feathers by rain and bleaching of feathers or bone. In many cases, we had live sightings of banded birds shortly before their deaths. Remains used in this analysis were classified on the basis of observations from field notes and examination of evidence collected at the site.

2. We assigned recent remains of birds for which we could determine sex and age (adult or yearling) to the 1/2 months in which we estimated they had died. We used these data from Comox Burn and Hardwicke Island combined to examine the seasonal pattern of predation, which was not significantly different at the two areas.

3. Kills may be underrepresented in April owing to smaller crews and less time in the field than in the rest of the breeding season, especially in early years of study.

4. Since age structure of males among prey remains appears unbiased, a balanced sex ratio in yearling remains may reflect that yearling females, many of which breed, are available to predators for a longer period than yearling males, many of which return to winter range in early to midsummer. Relative to males, females may be overrepresented.

5. Raptors typically, but not always, pluck flight and other feathers from a carcass and strip meat from the skeleton, usually breaking only thin or smaller bones. Mammals tend to chew feathers, mat them in clumps with saliva, and chew the bones, often breaking even the longbones.

6. Attacks are identified as such by clumps of, or scattered, feathers in greater numbers than would be expected from a moulting bird. They are most often back or rump feathers or rectrices, indicating the bird had been pounced upon by a mammal or struck from above by a raptor.

7. Other instances of ravens swooping at brood hens have been noted and might involve a search for chicks, but no instances of capture are known to us.

8. Corvids poke holes in eggs, leaving sharp edges around the holes after eating the contents; eggs eaten by mammals often are at least partially crushed (Einarsen 1956). Raptors, especially, may terminate nests by killing the hen, at or away from the nest, leaving the eggs undisturbed. Mammals are likely to eat the eggs if they kill a hen at the nest.

9. Potential mammalian nest predators at Comox Burn included weasels, pine marten, raccoon, red squirrel, black bear, mountain lion, wolf, and, prior to 1972, red fox. Those at Hardwicke Island included principally red squirrel and wolf, rarely weasel, black bear, and mountain lion. No mink (*Mustela vison*) were seen at either area, but they are potential nest predators.

10. Most shell remains were undoubtedly from blue grouse for only ruffed grouse and mallards have eggs which might be confused with those of blue grouse and be available there. The probability that most are from blue grouse is high, for we found 269 nests of blue grouse, only five of ruffed grouse, and one of a mallard (*Anas platyrhynchos*).

11. Nests of radioed birds and those deserted because of our activities were excluded from these analyses.

12. Ratings were based on amount of debris, such as logs, stumps, and perennial vegetation, that provided cover at the nest. A poor nest site had almost no cover, and the eggs (if the hen was absent) were readily visible from several angles. At a nest with moderate cover, the hen and (or) eggs were not visible from at least one, usually two, sides, nor usually, from above. At sites with good cover, it was difficult or impossible to see the hen or eggs even when one knew their location; in many cases, vegetation had to be moved to see the nest.

CHAPTER 20

Disease, Parasites, and Physical Anomalies

> *Almost any disturbance in the finely adjusted balance*
> *that constitutes health may lead to disease.*
>
> HW Schoening et al. (1956)

Disease is "any abnormal condition . . . that interferes with . . . vital physiological processes, caused by pathogenic microorganisms, parasites, . . ., etc." (Flexner and Hauck 1987, p. 564). It is, potentially, a major agent of morbidity and mortality that may have both immediate and evolutionary implications. Here, we identify diseases associated with pathogenic microorganisms (viruses, bacteria, and fungi) and parasites reported from blue grouse, recognizing, however, that pathogenicity may not be apparent with some infections. For example, these organisms may have negative, none, or positive impacts. We also consider physical anomalies noted by us or reported by others, some of which may have resulted from disease.

20.1 Viral, bacterial, and fungal diseases

Few viral and bacterial diseases have been identified in wild blue grouse, more in those held in captivity. In many cases, only symptoms or pathogenicities have been noted, and causative organisms are not known.

20.1.1 Wild birds

Cowan (1940) described what he considered to be a fatal disease of wild blue grouse, "avian cancer". Three birds shot by hunters on Vancouver Island, BC, had tumours associated with bare skin of the head (especially the eyelids). The disease was diagnosed as "low grade papillary carcinomata" (p. 312), probably caused by a filtrable virus, with transmission likely by biting flies. At least two other birds with such tumours were reported in the same area. With further study (Cowan 1942), these tumours were correctly identified as fowl pox, caused by *Epithelioma contagiosum* (synonym, *Poxvirus avium*; Karstad 1971). By 1941, at least nine cases had been seen in this area. We and our colleagues have observed superficial growths on the skin of at least 17 birds (Appendix 2), among >10 000 captured for marking or collected, mainly in coastal British Columbia. Seven were described as tumourlike, three wartlike, two molelike, and five scalelike. Pathogens are not known, and descriptions in field notes suggested that some may have been caused by fowl pox. Body mass was recorded for 16 of these birds, and in only two cases was it considered subnormal for the respective sex and age classes of the birds.

Deaths of three wild blue grouse have been attributed to aspergillosis (*Aspergillus fumigatus*), a fungus. One was emaciated and found dead on winter range (February) in westcentral Idaho (Caswell 1954*b*); a second, an adult male, was found dead on summer range at Sheep River (Boag 1958); and the third, an adult female, was observed wheezing and coughing over a period of 4 days on Cortes Island, BC, by R and N Kendel. This bird was found dead on 25 May 2002 (examination and diagnosis by FC Zwickel). In all cases, lungs and kidneys were mycotic.

Cowan (1942) examined a freshly dead adult male from Vancouver Island (1 April 1936) with enlarged, congested, and discoloured lungs and secondary bronchi occluded by a yellow cheesy mass. Otherwise, the bird was in good condition. Cowan diagnosed the probable cause of death as bronchopneumonia. The described symptoms suggest the possibility of aspergillosus.

Grouse are occasionally seen with what appear to be bacterial infections associated with wounds. Bendell (1955*c*) found 10 such cases among 60 chicks examined at Lower Quinsam in 1950, but saw none in 1951 or 1952. At Comox Burn, we captured a territorial adult male by hand (band 2658; 4 June 1969) that had a badly infected wing, apparently a result of bacterial invasion of a wound inflicted at first capture, 29 May. This bird lost 75 g in the 6 days between captures but was back on territory in 1970. In none of these cases were pathogens identified.

Few dead birds that have clearly died of disease have been found in the wild. Perhaps they hide and die in concealed places, decompose rapidly, or are soon consumed by scavengers. Diseased birds also may be taken by predators before succumbing to an infection.

20.1.2 Captive birds

More pathologies have been described in aviary birds than in those from the wild. Disease is a common problem in many aviary situations, often a result of crowding, unsanitary conditions, or exposure to pathogens of domestic galliforms.

Ten blue grouse trapped in northcentral Washington (18 July–3 August 1957) and held in an aviary at Washington State University died of ulcerative enteritis (Buss et al. 1958), all between 26 September and 7 October. Attempts to isolate enteric bacteria were unsuccessful, but other work suggests

Corynebacterium sp. may be involved in this disease (Peckham 1971).

Among 161 blue grouse held at the University of British Columbia [birds from Vancouver Island], 43% succumbed to disease (Stirling 1965). Among those deaths, 36% were attributed to gizzard erosion, 34% to aspergillosis, 26% to ulcerative enteritis, 3% to ulcerative gizzards, and 1% to proventriculitis. Except for aspergillosis, pathogens were not identified. Cooper (1977) also held birds from Vancouver Island in an aviary, at the University of Toronto. Among 49 deaths, 43% were attributed to ulcerative gizzards and 33% to aspergillosis. The others died of miscellaneous causes, including ulcerative enteritis, accidents, and unknown agents. Pathogens causing ulcerative enteritis and ulcerative gizzards were not identified.

We raised juveniles hatched from wild eggs, or taken from the wild at ≤10 days of age, in field aviaries on Vancouver Island (Zwickel and Bendell 1967*b*). Pathologies among 178 that died in summer included the following: 1 case of uraemia, 12 of excess yolk retention (may indicate incubation problems), 12 of hardened corelike cecal deposits, 19 of ascites, 22 of excess urates in the kidneys and ureters (52% of 42 examined for this condition), and 101 of inflamed intestines (57%). Lungs of 157 (95% of 166 examined for this condition) were congested to some degree, perhaps a secondary condition associated with later stages of dying. Many birds had multiple symptoms, and we do not know which might have been primary or secondary, e.g., 15 of 22 birds with excess urates in the kidneys and 6 of 12 with hardened cecal cores also had inflamed intestines. Attempts to isolate pathogens from some birds were all negative, but this may reflect problems in working with frozen tissues. Among 45 wild chicks collected for comparison, 4 had inflamed intestines (9%), 1 had corelike cecal deposits (2%), and 1 retained excess yolk (2%), indicating these conditions, at least, were not necessarily artifacts of the aviary.

20.2 Parasites

Parasites may live either on the outside of their hosts (ectoparasites) or inside their hosts (endoparasites). Different species and (or) groups, especially endoparasites, often inhabit specific organ systems, or portions of organ systems, with, in some cases, different life stages in different organs. We consider parasites by three major groupings: (1) ectoparasites, (2) haemoprotists (Kingdom Protista; unicellular parasites living in the vascular system) and haemofilarids (nematodes in the Superfamily Filarioidea and living in the vascular system), and (3) other endoparasites.

20.2.1 Ectoparasites

(a) *Species distributions*. Little has been done with ectoparasites of blue grouse beyond identification. Species reported to date include four ticks (Ixodoidea), two each in two genera, all from British Columbia; four bird lice (Mallophaga), in three genera; one flea (Siphonaptera); and two louse flies (Hippoboscidae), each in a separate genus (Table 20.1). Only the bird louse (*Lagopoecus obscurus*, *L. lyrurus* of Beer 1944) has

Table 20.1. Ectoparasites reported in blue grouse.

Group/species	Area[a] (sources)[b]
TICKS	
Haemaphysalis cinnabarina	BC (1)
Haemaphysalis leporispalustris	BC (1)
Ixodes auritulus	BC (1); BC coast (2)
Ixodes ricinus	BC (1)
BIRD LICE	
Degeeriella perplexa (perhaps = *Lagopoecus* sp.; see text)	WA coast (3)
Goniodes merriamanus	AB (4); MT (5); WY (5); location not specified (6)
Goniodes simoni	Location not specified (6)
Lagopoecus obscurus (likely syn. *L. lyrurus* of Beer 1944)	AB (4); BC coast (2, 5); BC interior (5); CA coast (5); MT (5); WA coast (5); WA interior (3, 5); location not specified (6)
FLEA	
Ceratophyllus diffinis	AB (4); BC (7); BC coast (2)
LOUSE FLIES	
Ornithoica vicina	BC (8)
Ornithomya anchineuria (likely syn. *O. fringillina*, according to Maa (1969))	AB (4); BC (8, 9); BC coast (2); WA interior (3, 10)

Note: AB, Alberta; BC, British Columbia; CA, California; MT, Montana; WA, Washington; WY, Wyoming. If more than one subspecies of blue grouse occurs within a jurisdiction, the region in which a collection was made is noted, if known.
1, Hearle (1938); 2, Bendell (1955*c*); 3, Beer (1944); 4, Holmes and Boag (1965); 5, Emerson (1951); 6, Malcomson (1960); 7, Holland (1984); 8, Bequaert (1954); 9, Spencer (1938); 10, Schotellius (1951*b*).

been collected widely and found on coastal and interior subspecies of blue grouse. The louse fly (*Ornithomya anchineuria = O. fringillina*) and the flea (*Ceratophyllus diffinus*) also have been found on coastal and interior birds, but over a more restricted range. The bird louse (*Goniodes merriamanus*) may be confined to Rocky Mountain populations, but this conclusion is speculative because of limited collections of ectoparasites. A lack of records from many areas may reflect the activities of biologists rather than the absence of ectoparasites. Although not specifically reported as parasites of blue grouse in the literature, there are a number of blood-sucking flies that attack birds. These include some species of blackflies (Simuliidae), no-see-ums (Ceratopogonidae), and mosquitoes (Culicidae). Some species of black flies and no-see-ums are known vectors of some haemoprotists found in blue grouse (see 20.2.2(b)).

(b) *Alternate hosts*. Alternate hosts provide a reservoir and possible source of infection for a given species. Most ectoparasites of blue grouse also have been found on other North American tetraonines (Fig. 20.1). *Ixodes auritulus* was reported from an unspecified species of grouse in British Columbia (Gregson 1956), and *Ixodes ricinus*, *D. perplexa*, *G. merriamanus*, and *G. simoni* appear not to have been found on other tetraonines. We suspect most ectoparasites of blue grouse will be found on other tetraonines.

(c) *Prevalence and intensities of infection*. The most complete information on ectoparasites of blue grouse is from birds at Lower Quinsam (Bendell 1955*c*). Among 103 adults and yearlings, 38% carried *L. obscurus* (1–300/bird); 11%, *Ceratophyllus diffinus* (1–4/bird); and 2%, *O. anchineuria* (1–2/bird). Among 107 chicks, 20% carried *L. obscurus* (1–50/bird); none, *C. diffinus*; and 7%, *O. anchineuria* (1–2/bird). Except *O. anchineuria*, infection rates were lower in chicks than in yearlings and adults. No author has indicated ectoparasites might be serious pathogens of blue grouse, although Hearle (1938) suggested tick-transmitted diseases may contribute to fluctuations of grouse (species unspecified) in British Columbia.

Other data on intensities of infections are sparse. Beer (1944) counted 92 *Degeeriella perplexa* on an adult male from coastal Washington and noted little injury other than minor irritation [*D. perplexa* may be a misidentification, for other than this report this genus appears to have been correctly identified only from Falconiformes (AW Shostak, pers. comm.); may be *Lagopoecus*?]. Beer found *L. obscurus* (= *L. lyrurus*) on 1 of 111 birds in northcentral Washington. This bird was held in captivity and was weak at time of death [caused by injury], which may have contributed to a "large infestation" (p. 91). Beer also found *O. anchineuria* on a bird in northcentral Washington but considered this an unusual record. Boag (1958) reported the incidence of mallophagan infestation to be high in blue grouse in southwestern Alberta, but provided no data on prevalence or intensity of infestations. These records are too sparse to speculate on the effects of ectoparasites on this host.

20.2.2 Haemoprotists and haemofilarids

(a) *Species distributions*. Parasites of the vascular system of blue grouse have received most study. Four genera of haemoprotists (three with one species each and one with two species) and unidentified microfilariae (motile embryonic nematodes, Nematoda) have been identified in blood films (Table 20.2). Except *Plasmodium*, all other haemoprotists and microfilariae have been found at virtually all sites sampled from southeast Alaska, Yukon Territory, and Alberta in the north, to Colorado, Nevada, and northern California in the south (Williams et al. 1980; Mahrt et al. 1991). Most exceptions reflect small samples (<10 birds), but absence of *Haemoproteus mansoni* from a sample of 68 birds in central interior British Columbia may indicate absence of a suitable vector (Mahrt et al. 1991). *Plasmodium* spp. have been identified only from Montana, Colorado, and coastal British Columbia, and failure to detect them elsewhere may indicate a low level of prevalence (see below).

Mahrt et al. (1991) considered it important that the same species of haemoprotists infect blue grouse throughout their range [except, perhaps, *Plasmodium* spp.] in habitats ranging from sea level to subalpine and from rain forest to high desert. This host–parasite association may be explained by intermediate hosts sharing the same distribution as blue grouse, by a low specificity of this grouse to haematophagous insect vectors, and (or) by a wide tolerance by it to blood parasites.

(b) *Vectors*. Suitable vectors are necessary for transmission of haemoprotists from host to host. Blackflies are known to transmit *Leucocytozoon*, *Trypanosoma*, and microfilariae; no-see-

Fig. 20.1. Alternate tetraonine hosts of ectoparasites reported from blue grouse. Cross-hatching indicates presence in the indicated species. Note: *Degeeriella perplexus* perhaps may be *Lagopoecus perplexus* (see text). RUGR, ruffed grouse; SPGR, spruce grouse; SAGR, sage-grouse; SHGR, sharp-tailed grouse; PRCH, prairie-chicken; WIPT, willow ptarmigan; ROPT, rock ptarmigan; WHPT, white-tailed ptarmigan. References: Gross (1930), Bump et al. (1947), Patterson (1952), Hillman and Jackson (1973), Wallestad (1975), Wheeler and Threlfall (1989).

	RUGR	SPGR	SAGR	SHGR	PRCH	WIPT
Haemaphysalis cinnabarina	▨	▨	▨	▨	▨	
Haemaphysalis leporispalustris	▨	▨	▨	▨	▨	
Ixodes auritulus	▨					
Ixodes ricinus						
Degeeriella perplexus				?		
Goniodes merriamanus						
Goniodes simoni						
Lagopoecus obscurus	▨	▨				▨
Ceratophyllus diffinus	▨					
Ornithoica vicina	▨					
Ornithomya anchineuris	▨	▨		▨		▨

Table 20.2. Haemoprotists and microfilariae reported in blue grouse.

Species	Area[a] (sources)[b]
Trypanosoma avium	AK (1); BC coast (1, 2); BC interior, CA coast, CO, eastern NV, MT, OR interior, WA interior, YT (1)
Trypanosoma sp.	AB (3); BC coast (4–8); CO (9); MT (10); WA interior (11)
Haemoproteus mansoni (syns. *H. canachites*, *H. dendragapi*, White and Bennett (1979))	AK (1); BC coast (1, 2, 7, 8, 12); BC interior, CA coast (1), CO (1,13), MT, eastern NV, OR interior, WA interior (1)
Haemoproteus sp.	AB (3); BC coast (4–6); CO (9); MT (10); WA interior (11)
Leucocytozoon bonasae (syn. *L. lovati* of Mahrt et al. (1991))	AK (1); BC coast (1, 2, 7, 8, 12); BC interior, CA coast, CO, MT, eastern NV, OR interior, WA interior, YT (1)
Leucocytozoon sp.[c]	AB (3); BC coast (4–6, 12); CO (9); MT (10); WA interior (11)
Plasmodium pedioecetii (syn. *P. pedioecetae*, Stabler and Kitzmiller (1974))	CO (9, 14); MT (10)
Plasmodium circumflexum	BC (15)
Plasmodium sp.	BC (15); BC coast (8)
Microfilariae	AB (3); BC coast (1, 2, 4–6); BC interior (1); CO (1, 9); MT (1, 10); eastern NV, OR interior, WA interior, YT (1); WA interior (11)

[a] AB, Alberta; AK, Alaska; BC, British Columbia; CA, California; CO, Colorado; MT, Montana; NV, Nevada; OR, Oregon; WA, Washington; YT, Yukon Territory. If more than one subspecies of blue grouse occurs within a jurisdiction, the region in which collection was made is noted, if known.

[b] 1, Mahrt et al. (1991); 2, Williams et al. (1980); 3, Holmes and Boag (1965); 4, Fowle (1946); 5, Adams and Bendell (1953); 6, Bendell 1955*c*); 7, Woo (1964); 8, King (1971); 9, Stabler et al. (1974); 10, Stabler et al. (1969); 11, Schotellius (1951*b*); 12, Allan (1984); 13, White and Bennett (1979); 14, Stabler and Kitzmiller (1976); 15, Bennett et al. (1989).

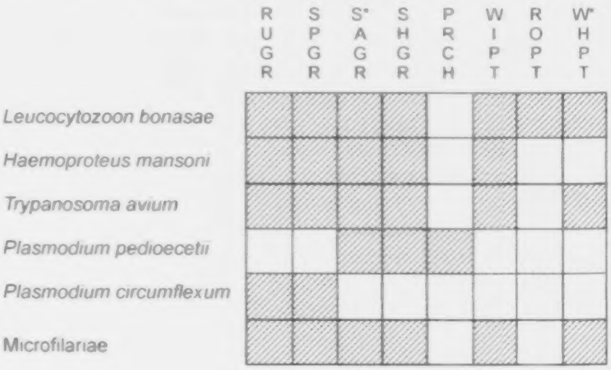
[c] Allan and Mahrt (1987) found round and elongate *Leucocytozoon* gametocytes in blue grouse on Hardwicke Island. They suggest these may be different species.

ums are known to transmit *Haemoproteus*. Among 10 species of blackflies identified at Comox Burn, *Simulium aureum* and *Cnephia minus* harbour avian haemoprotists. Among four species of no-see-ums there, *Culicoides crepuscularis* harbours *Haemoproteus* (Williams et al. 1980). *S. aureum* and *C. minus* were found with developing and infective *Leucocytozoon* at Comox Burn and served as vectors for microfilariae in other areas of Vancouver Island (Gibson 1965). Mahrt (1982) identified 19 species of blackflies (Simuliidae) at Hardwicke Island, including *S. aureum*, but not *C. minus*. *S. aureum* is widespread, often abundant, and may be a principal vector of haemoprotists over much of the range of blue grouse.

(c) *Alternate hosts*. All haemoprotists of blue grouse have been reported from other North American tetraonines, at least at the generic level (Fig. 20.2). *H. mansoni* also has been reported in four European tetraonines: hazel grouse, black grouse, capercaillie, and red grouse (White and Bennett 1979).

Haemoprotists of blue grouse appear to show low host specificity among the tetraonines. Failure to find these taxa in some tetraonines, e.g., white-tailed ptarmigan in Colorado (Stabler et al. 1974) and willow ptarmigan in northwestern British Columbia (Mahrt 1981), may reflect an absence of suitable vectors. Microfilariae of tetraonines usually have not been identified to species, and whether low tetraonine specificity also applies to them has not been determined. Gibson's (1967) suggestion that *Splendidofilaria pectoralis* occurs in interior, but not coastal, blue grouse in British Columbia indicates these nematodes (and their microfilariae) might be more host specific than the haemoprotists.

Fig. 20.2. Alternate tetraonine hosts of haemoprotists reported from blue grouse. Cross-hatching indicates presence in the indicated species. RUGR, ruffed grouse; SPGR, spruce grouse; SAGR, sage-grouse; SHGR, sharp-tailed grouse; PRCH, prairie-chicken; WIPT, willow ptarmigan; ROPT, rock ptarmigan; WHPT, white-tailed ptarmigan. References: Cowan and Peterle (1957), Stabler et al. (1974), Stabler and Kitzmiller (1976), Mahrt (1981), Stabler and Miller (1984), Bennett et al. (1989). *Sage-grouse and white-tailed ptarmigan are known only to the generic level.



	RUGR	SPGR	S*AGR	SHGR	PRCH	WIPT	ROPT	W*HPT
Leucocytozoon bonasae	▨	▨	▨	▨		▨	▨	▨
Haemoproteus mansoni	▨	▨	▨	▨		▨		
Trypanosoma avium	▨	▨	▨	▨		▨		▨
Plasmodium pedioecetii			▨	▨	▨			
Plasmodium circumflexum	▨	▨						
Microfilariae	▨	▨	▨	▨		▨		▨

(d) *Prevalence of infections*. Williams et al. (1980) summarized information on prevalences of haemoprotists from 10 sites: 1 in southwest Alberta, 6 in coastal British Columbia, 1 in Colorado, 1 in westcentral Montana, and 1 in northcentral Washington. Among 2794 birds examined (all studies combined, 85% from British Columbia), prevalences were as follows: *Leucocytozoon bonasae*, 79% (median, among sites = 82%; range = 18%–100%); *H. mansoni*, 52% (median = 51%; 7%–92%); *Trypanosoma avium*, 55% (median = 54%; 5%–84%); *Plasmodium* sp., 0.2% (median = 4% (three positive studies only); 0%–6%), and microfilariae, 42% (median = 37% (nine positive studies only); 0%–82%). Wide ranges may reflect, at least in part, relatively small samples or variations in the proportions of different sex and age classes of grouse among samples (see below).

Mahrt et al. (1991) surveyed prevalences at 11 sites from Alaska and Yukon Territory, to Colorado, Nevada, and California. Combining samples from all sites ($n = 333$), prevalences were *L. bonasae* (*L. lovati* of Mahrt et al.), 90% (range among sites = 80%–94%); *H. mansoni*, 29% (0%–38%); *T. avium*, 46% (32%–51%); and microfilariae, 29% (15%–37%); ranges are for only the five sites in which samples of birds were ≥10. *Plasmodium* was not found. Among all birds, 95% were infected with one or more species. Samples from most areas were small (≤13) and, along with variations in the proportions of different sex and age classes within each, likely account for much of the variation in ranges. This survey and that of Williams et al. (1980) show that *L. bonasae*, *H. mansoni*, *T. avium*, and microfilariae are widespread and that, within most areas, they are common in terms of prevalence. Mahrt et al. (p. 484) predicted, "All populations of blue grouse likely will be found infected with *L. lovati* and *T. avium*, and most, with *H. mansoni* and microfilaria."

Most workers have not compared prevalences between males and females, but Williams et al. (1980) did so for adults and yearlings. Based on data in their Tables 3–6, there were no significant differences between sexes in mature birds (yearlings and adults) in the incidence of *L. bonasae* [1a], *T. avium* [1b], or *H. mansoni* [1c], although the latter (males 55%, females 61%) approached significance. Males had the highest incidence of microfilariae (males 64%, females 55%), the only significant difference between sexes [1d]. King (1971), working in subalpine Vancouver Island, found prevalences of all principal haemoprotists except *Haemoproteus* similar to those on nearby lowlands. *Haemoproteus* was less prevalent than on the lowlands and was not detected in any of the five females examined.

Mature birds were more heavily infected than juveniles with all of the principal haemoprotists in all studies shown. Rate of infection of adults with *L. bonasae* was consistently high (≥85%), and with *T. avium*, moderately high (≥64%), in the three studies with large samples (Table 20.3). Prevalences of *H. mansoni* and microfilariae varied more, but with one exception (microfilariae in Montana) always exceeded 58%. Juveniles showed greater variation among studies, and levels of infection were lower than in adults. Variation may relate to the proportions of chicks of different ages sampled, for some may not have yet been infected, or have had prepatent infections. In general, prevalence levels of all taxa increased from spring to mid or late summer, perhaps partly a result of the emergence of, or increase in size of, vector populations.

(e) *Multiple infections*. Among 1707 grouse examined at Comox Burn, 84% were infected with one or more of the above taxa (Williams et al. 1980). Quadruple infections with the four principal taxa were found in 24% of all birds; 18% had only *L. bonasae*; and lesser percentages with single, double, or triple infections in various combinations.

Blue grouse in western Montana also showed a high rate of multiple infection. Among 274 birds, 31% had double, 25% triple, and 18% quadruple infections (Stabler et al. 1969). In northcentral Washington, four of six adults, but only one of nine juveniles, had multiple infections (Schottelius 1951*b*).

(f) *Intensity of infections*. Fowle (1946), Bendell (1955*c*), and Williams et al. (1980) provided information on intensity of infections from blue grouse on Vancouver Island. Fowle (p. 708) found trypanosomes in small numbers in only two birds and, "*Leucocytozoon* seldom exceeded two parasites per 1000 blood cells". *Haemoproteus* was most common, ranging from 1 to 27 (mean = 12) per 1000 red blood cells (rbc) in June, July, and August. No microfilariae were found among 36 juveniles, and intensities of infection by the three protists were lower in juveniles than adults.

Table 20.3. Prevalence (in %) of haemoprotists and microfilariae in adult (includes yearlings) and juvenile blue grouse.

	L. bonasae		*H. mansoni*		*T. avium*		Microfilariae	
Area, source	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult	Juvenile
VANCOUVER ISLAND								
Fowle 1960[a]	22	14	52	48	4	5	22	0
Bendell 1955*c*	85	38	97	66	77	20	80	0
Williams et al. 1980[b]	96	52	59	17	70	29	58	6
WESTERN MONTANA								
Stabler et al. 1969	97	35	61	6	64	11	42	2

Note: Sample sizes as follows: Fowle, 23 adults, 21 juveniles; Bendell, 174 adults, 89 juveniles; Williams et al., 1025 adults, 682 juveniles; Stabler et al., 219 adults, 55 juveniles.

[a] Fowle identified species only to generic level. Samples were from Lower Quinsam and Cowichan Lake areas combined.

[b] Percentages calculated by us from data in Tables 3–6 of Williams et al.

Bendell (1955*c*) reported 1–2 *Leucocytozoon* and 1–500 *Haemoproteus*/1000 rbc and 1–20 *Trypanosoma* and 1–25 microfilariae/blood smear in mature birds. He found 1 *Leucocytozoon*/1000 rbc, 1–50 *Haemoproteus*/1000 rbc, 1–10 *Trypanosoma*/blood smear, and no microfilariae in chicks.

Williams et al. (1980) found 0.8–1.2 *Leucocytozoon*, 2.7–11.1 *Haemoproteus*, 0.1–0.2 *Trypanosoma*, and 0.2 microfilariae/1000 rbc among various sex and age classes, with, usually, little difference between juveniles and mature birds. Mature females tended to be more heavily infected with *Haemoproteus* than mature males, but no sex differences were apparent within other genera.

(g) *Age of acquisition*. Experimental exposure of 75 chicks to *L. bonasae*, *H. mansoni*, and *T. avium* at Comox Burn resulted in detectable infections at 45–56 days in 5 birds, 45–50 days in 3 birds, and 28–56 days in 10 birds, respectively (Williams et al. 1980). There, where peak hatch usually occurs in mid June, *L. bonasae*, *H. mansoni*, and *T. avium* were first detected in wild chicks in the fourth week of July in 3 of 4 years, 2–3 weeks earlier in a year of early hatch. Microfilariae were first detected 5–9 weeks after peak hatch, depending on year.

In western Montana, Stabler et al. (1969) first found *Trypanosoma* in blood of wild chicks at 3 weeks, *Leucocytozoon* at 5 weeks, *Haemoproteus* at 8 weeks, and microfilariae at 11 weeks, of age. In northcentral Washington, Schottelius (1951*b*) found no haemoprotists in chicks until they were 7 weeks old, and only *Leucocytozoon* and *Haemoproteus* were seen. Clearly, ages at which chicks are sampled will have a strong influence on prevalence levels.

(h) *Pathology*. No author has suggested haemoprotists or haemofilarids of blue grouse might be pathogenic. For example, Bendell (1955*c*, p. 203) noted, "... despite the high percentage and degree of infections recorded for blood parasites no effect on the host was observed." Haemoprotists and haemofilarids appear to be living in blue grouse more as commensals than as pathogens.

20.2.3 Other endoparasites

One other protist, *Eimeria oreoecetes*, has been reported in blue grouse. Oocysts of this species were found in feces of 2 of 16 blue grouse and 29 of 455 white-tailed ptarmigan in Colorado (Stabler et al. 1979). Location of the endogenous cycle is not known, but related species usually inhabit the intestine or ceca in other galliforms. No other coccidians, although common in some galliforms, have been reported. At least 17 species of helminths, other than microfilariae, are known from blue grouse, most inhabiting specific regions of the gastrointestinal tract (Table 20.4).

(a) *Species distributions*. All studies of helminths (parasitic species of the Nemathelminthes and Platyhelminthes) of blue grouse have been in the central area of distribution of this host (in a north–south sense). Seven species have been reported only from coastal areas, six only from interior areas, and four from both (Table 20.4). Most do not appear to have the same cosmopolitan distribution over the range of this host as the haemoprotists, but helminths have not received the same degree of attention. Nothing is known about helminths of more northern and southern populations.

(b) *Life cycles*. Some helminths have direct life cycles, i.e., no intermediate hosts or vectors. These include the nematodes *Ascaridia bonasae* and *Heterakis gallinarum*, in which infective eggs are picked up by birds with their food or water (Wehr 1971). The gapeworm, *Syngamus trachea*, may be attained either directly or through consumption of infected earthworms (Wehr 1971).

(c) *Vectors and intermediate hosts*. Only a limited amount of work has been done to identify vectors and intermediate hosts of helminths of blue grouse, and one often must rely on generalizations from work with related species.

Blackflies are likely vectors of *Splendidofilaria pectoralis* and *Chandlerella chitwoodae* (Gibson 1967; Wehr 1971). Intermediate hosts of *Dispharynx nasuta* and *Plagiorhynchus formosus* are likely sow bugs and (or) pill bugs (Isopoda); of *Cheilospirura spinosa*, beetles or grasshoppers; and of *Brachylaima fuscata* and *Davainea tetraoensis*, gastropods (Gastropoda, Casperson 1963). Species of *Raillietina* in chickens and turkeys may be acquired by eating ants or beetles (Gardiner 1956), and one or the other, or both, are probable intermediate hosts of *R. variabilis*. Those of *Rhabdometra* are probably invertebrates—likely ants and (or) beetles (CE Braun, pers. comm.).

(d) *Alternate hosts*. Among helminths of blue grouse, all but *Plagiorhynchus formosus* and *Molinacuaria bendelli* have been reported from other North American grouse (Fig. 20.3). Most show low host specificity among the tetraonines. The range of blue grouse overlaps with all North American grouse except prairie-chickens, so, in areas of sympatry, all except the latter serve as potential reservoirs for infecting them. A lower incidence of blue grouse helminths in most tetraonines [other than ruffed grouse] may reflect less work on parasites of these species. Other groups of birds carry some helminths of blue grouse, and most North American tetraonines harbour species that have not been reported in them.

(e) *Prevalence of infections*. Prevalences of helminths in blue grouse are often high, usually >60% in juveniles, yearlings, and adults (Table 20.5). The sole exception is King's (1971) subalpine population in eastcentral Vancouver Island, with an infection rate of only 7% among yearlings and adults. This may reflect an absence, or low density, of suitable vectors or intermediate hosts for in nearby lowlands, e.g., Lower Quinsam and Campbell River, prevalence of even a single species usually exceeded this level.

Most of what we know about prevalences of different helminths is from Vancouver Island (Table 20.5). Here, grouse collected in spring and summer at Lower Quinsam (1950–1952; Bendell 1955*c*) and gut tracts collected at Campbell River from birds shot by hunters in autumn (1957–1962; Casperson 1963) provided the only relatively large samples.[1] *Dispharynx nasuta* and *P. formosus* had higher rates of infection in juveniles than in yearlings and adults in both sets of data. Both parasites also had lower rates of infection in juveniles in autumn than in spring and summer. Casperson thought this might be caused by mortality of juveniles before autumn, but one cannot rule out the possibility these differences resulted from variations among years in which samples were collected, or seasonal variations in the prevalence of these parasites. This question is still open.

Table 20.4. Helminths (for microfilariae, see Table 20.2) reported in blue grouse and organs, or organ systems, with which they are usually associated.

Organs/species	Area[a] (sources)[b]
SUBCUTANEOUS CONNECTIVE TISSUE	
Splendidofilaria pectoralis	BC interior (1)
COELOMIC CONNECTIVE TISSUE	
Chandlerella chitwoodae (syn. *Splendidofilaria flexivaginalis* of Gibson (1965))	BC coast (2)
INTRAMUSCULAR	
Physaloptera sp. (larvae)	AB (3), CO (4)
TRACHEA	
Syngamus trachea	BC coast, in captivity (5)
PROVENTRICULUS	
Dispharynx nasuta	BC coast (6–8)
GIZZARD	
Cheilospirura spinosa (syn. *Acuaria spinosa*, Wong et al. (1990))	AB (9); BC coast (6, 8, 10)
Cheilospirura sp.	WA interior (11, 12)
Molinacuaria bendelli (syns. *Ancyracanthopsis bendelli* of Adams and Gibson (1969), *Yseria* sp. of Bendell (1955*c*) and Casperson (1963))	BC coast (6, 10, 20)
SMALL INTESTINE	
Brachylaima fuscata (likely syn. *B.* sp. of Jensen (1962))	BC coast (7, 10)
Davainea proglottina[c]	BC coast, interior (10)
Davainea tetraoensis[c,d] (*D. proglottina* of Boag (1958) and likely *D.* sp. of Boag (1964))	AB (13, 14)
Davainea sp.[c]	WA interior (12)
Raillietina sp.[c–e]	AB (13, 14); ID (16); WA interior (11, 12, 17)
Rhabdometra nullicollis[d] (*R. odiosa* of Boag (1958) and *R.* sp. of Boag (1964))	AB (13, 14); BC coast (6, 8, 10); WA interior (11, 17); BC (18)
Rhabdometra odiosa (may be syn. with *R. tomica* of Russian black grouse, Mahon (1956))	BC (18); WA interior (12)
Rhabdometra sp.	WA interior (12)
Plagiorhynchus formosus[c]	BC coast (6, 10)
Ascaridia bonasae	BC coast (6, 8, 10); area? (19)
Unidentified cestodes	CO (4)
CECA	
Heterakis gallinarum (syn. *H. gallinae*, Wong et al. (1990))	WA interior (11, 17)
CLOACA	
Urogonimus sp.	AB (14, 15)

[a] AB, Alberta; BC, British Columbia; CO, Colorado; WA, Washington. If more than one subspecies of blue grouse occurs within a jurisdiction, the region in which collection was made is noted, if known.

[b] 1, Gibson (1967); 2, Gibson (1965); 3, Mitchell and Bigland (1960); 4, CE Braun, pers. comm.; 5, FC Zwickel, pers. observ.; 6, Bendell (1955*c*); 7, Jensen (1962); 8, King (1971); 9, DA Boag, pers. comm.; 10, Casperson (1963); 11, Beer (1944); 12, Schotellius (1951*b*); 13, Boag (1958); 14, Holmes and Boag (1965); 15, Boag (1964); 16, Caswell (1954*b*); 17, Buss et al. (1958); 18, Mahon (1956); 19, Mawson (1956); 20, Adams and Gibson (1969).

[c] Duodenum.

[d] Ileum.

[e] Jejunum.

Cheilospirura spinosa of Bendell (1955*c*) and Casperson (1963) included what they tentatively identified as *Yseria* sp., morphologically similar to *C. spinosa* and later described by Adams and Gibson (1969) as *Ancyracanthopsis bendelli* n. sp. (now *Molinacuaria bendelli* (Wong et al. 1990)). *Molinacuaria bendelli* was the most common helminth in Casperson's collections and was more prevalent in juveniles than yearlings and adults, opposite to that in Bendell's samples. *Rhab-*

Fig. 20.3. Alternate tetraonine hosts of helminths reported from blue grouse. Cross-hatching indicates presence in the indicated species. RUGR, ruffed grouse; SPGR, spruce grouse; SAGR, sage-grouse; SHGR, sharp-tailed grouse; PRCH, prairie-chicken; WIPT, willow ptarmigan; ROPT, rock ptarmigan; WHPT, white-tailed ptarmigan. References: Gross (1930), Bump et al. (1947), Patterson (1952), Bendell (1955*c*), Holmes and Boag (1965), Gibson (1967), Braun and Willers (1967), Harper et al. (1967), Evans (1968), Hillman and Jackson (1973), Wallestad (1975), Pence and Sell (1979), Wong et al. (1990).

	RUGR	SPGR	S*AGR	SHGR	PRCH	WIPT	ROPT	W*HPT
Splendidofilaria pectoralis	▨	▨		▨				
Chandlerella chitwoodae	▨							
Physaloptera sp.	▨			▨				
Syngamus trachea	▨							
Dispharynx nasuta	▨			▨	▨			
Cheilospirura spinosa	▨		▨	▨	▨			
Brachylaima fuscata	▨	▨	▨	▨		▨	▨	▨
Davainea tetraoensis	▨	▨				▨	▨	▨
Raillietina variabilis	▨	▨			▨			
Rhabdometra nullicollis	▨	▨	▨	▨	▨		▨	
Rhabdometra odiosa	▨	▨		▨	▨			
Plagiorhynchus formosus								
Ascaridia bonasae	▨							
Molinacuaria bendelli								
Heterakis gallinarum	▨		▨	▨	▨	▨	▨	▨
Urogonimus sp.	▨	▨						

dometra sp. and *A. bonasae* followed the same pattern; i.e., less prevalent in juveniles than yearlings and adults in spring–summer samples, but more prevalent in autumn samples. This may reflect a high proportion of chicks in spring and summer samples that had not yet been infected or that carried prepatent infections. In this area, a higher proportion of juveniles appeared to be entering winter with these genera than in yearlings and adults.

Although sample sizes from northcentral Washington are unknown (Beer 1944) or small (n = 19; Schottelius 1951*b*), data indicate that infection rates with *Rhabdometra* were similar to those of birds on Vancouver Island (Table 20.5). Rates of infection with *Davainea* and *Raillietina* were relatively low (≤21%).

(f) *Intensity of infections*. Some reports of intensity of infections with helminths are more or less anecdotal and not quantified. For example, in southwest Alberta intensities of infections with tapeworms may range from, "one or two worms to an almost virtual blockage of the gut tract" (Boag 1958, p. 62). Other authors simply reported the number of a given species found in one individual, providing no information on norms, or ranges, e.g., Beer (1944) found 12 *H. gallinarum* in the ceca of a juvenile in northcentral Washington. Ranges in numbers of helminths found within a sample of hosts, or the maximum number found in an individual are sometimes reported and usually represent the most comprehensive information available (Table 20.6). Means, medians, and (or) ranges, were usually not presented, making interpretations difficult.

(g) *Age of acquisition*. All helminths of blue grouse (Table 20.4) have been found in juveniles in their first months of life, some within days of hatch. Ages of chicks at first detection reported for some species are as follows:

D. nasuta—<1 week of age (Bendell 1955*c*); 8 days of age, experimental infection in laboratory (Jensen 1962)

Raillietina sp.—16 days of age (Beer 1944); <2 weeks of age (Schottelius 1951*b*)

Rhabdometra nullicollis—12 days of age (Beer 1944)

P. formosus—<1 week of age (Bendell 1955*c*)

Clearly, young blue grouse are susceptible to infection with at least some helminths shortly after hatch.

(h) *Pathology*. Among the helminths, most appear relatively benign, others to have severe pathological effects. Those for which detectable pathologies have been reported are as follows:

Splendidofilaria pectoralis—yellowing of skin; in heavy infections, inflammation and thickening of subcutaneous tissue; no indication heavy infections are seriously detrimental (Gibson 1967).

Syngamus trachea—birds have breathing difficulties, blood clots in trachea (birds in captivity, pers. observ.).

D. nasuta—chicks with ≥50 *D. nasuta* and 1–5 *P. formosus* may appear healthy (Bendell 1954); chicks: in infestations of 100–300 worms proventriculus is enlarged and inflamed, proliferated into long fibrous shreds; buildup of mucus in lumen may create a barrier to passage of food; birds emaciated and weak (Bendell 1955*c*). Experimental infection with 16–22 worms fatal if administered to chicks <2 weeks of age; feather growth retarded in chicks with >10 worms at <10 weeks of age; gain in body mass less in infected than control chicks; severity of infection proportional to number of worms and age of host; no pathological symptoms in adults (Jensen 1962).

C. spinosa—as few as 1–5 worms may cause considerable injury to gizzard wall, especially near opening between proventriculus and ventriculus (Beer 1944). No evidence of pathology (Casperson 1963).

Rhabdometra spp.—petechial hemorrhages at point of attachment to wall of intestine (*R. odiosa*, Schottelius 1951*b*); gut occluded in an adult male, with large hemorrhagic areas on walls of intestine; clear mechanical damage; body mass subnormal (*R.* sp., Schottelius 1951*b*). Gut may be more or less

Table 20.5. Prevalence of helminths (%) reported in blue grouse; adult includes yearlings.

Species and location (sources)[a]	Juveniles % (*n*)	Adult % (*n*)	Total % (*n*)
ALL HELMINTHS COMBINED			
Campbell River (1)	89 (231)		
Vancouver Island, subalpine (2)		7 (110)	
Northcentral WA (3)			63 (19)
Southwestern Alberta (4, 5)	70 (50)	68 (82)	68 (133)
INDIVIDUAL SPECIES			
Dispharynx nasuta			
Lower Quinsam (6)	64 (107)	4 (103)	34 (210)
Campbell River (1)	21 (71)	8 (48)	20 (119)
Cheilospirura spinosa			
Lower Quinsam (6)[b]	10 (107)	22 (103)	16 (210)
Campbell River (1)[b]	72 (71)	44 (48)	61 (119)
Northcentral WA (3)			5 (19)
Davainea sp.			
Northcentral WA (3)			21 (19)
Raillietina sp.			
Northcentral WA (3)			16 (19)
Northcentral WA (7)			14 (?)
Rhabdometra sp.			
Lower Quinsam (6)	21 (107)	39 (103)	30 (210)
Campbell River (1)	31 (71)	17 (48)	25 (119)
Northcentral WA (3)			26 (19)
Northcentral WA (7)			44 (?)
Plagiorhynchus formosus			
Lower Quinsam (6)	50 (107)	0 (103)	25 (210)
Campbell River (1)	11 (71)	2 (48)	8 (119)
Ascaridia bonasae			
Lower Quinsam (6)	4 (107)	14 (103)	9 (210)
Campbell River (1)	11 (71)	2 (48)	9 (119)

[a] 1, Casperson (1963); 2, King (1971); 3, Schotellius (1951*b*); 4, Boag (1958); 5, Boag (1964); 6, Bendell (1955*c*); 7, Beer (1944).

[b] Includes *Molinacuaria bendelli* (see text).

occluded (*R. odiosa*, Boag 1958). Body mass subnormal in an immature female (*R. nullicollis*, Beer 1944) and two adult males (King 1971). No pathology noted (*R. nullicollis*, Casperson 1963).

P. formosus—head embedded in wall of gut with obvious damage to tissues, or gut may be perforated and worms free in coelom; gut usually constricted and thrown into a tight coil at site of infection, apparently blocking the lumen (Bendell 1955*c*).

Among these species, *D. nasuta*, *Rhabdometra odiosa* and *R. nullicollis*, and *P. formosus* appear to have the greatest potential for causing significant problems. *D. nasuta* and *P. formosus*, however, have been reported in blue grouse only from Vancouver Island. Pathologies have not been noted for most species of helminths, although some may cause disease in other galliforms, e.g., *D. proglottina* in domestic chickens (Crawley 1922). But there has been only a limited amount of study devoted to helminths. As well, debilitated birds may be taken by predators, may die and be cleaned up by scavengers, may decompose rapidly, or not be found.

20.3 Physical anomalies

Anomalies may be innate or result from external forces, e.g., from accidents, predator-induced wounds, or disease. Some are life-threatening, others benign; some are recurring, others represent single incidents. We document those we and our colleagues have noted in the handling of >10 000 blue grouse, mainly in coastal British Columbia, in Appendix 2. Cause is often not known, or conjectural, because it was recorded on a field record and the bird released. Assuming we have noted most anomalies, we summarize their incidences here.[2]

Table 20.6. Intensity of infections of blue grouse with helminths (range, or maximum number, of worms reported per host).

Species (source)[a]	No. infected	Range or maximum no.
Splendidofilaria pectoralis (1)	13	1–48
Physaloptera sp. (larvae) (2)	1	37
Dispharynx nasuta (3)		
Yearlings and adult	4	1–6
Juveniles	68	1–430
Cheilospirura spinosa		
Lower Quinsam (3)[b]	34	1–5
Northcentral WA (4)	4	1–5
Davainea sp. (5)	4	51
Raillietina sp.(4)	15	53
Rhabdometra sp.		
Lower Quinsam (3)	66	1–20
Northcentral WA (4)	48	93
Northcentral WA (5)	5	44
Plagiorhynchus formosus (3)[c]	53	1–33
Ascaridia bonasae (3)[d]	18	1

[a] 1, Gibson (1967); 2, Mitchell and Bigland (1960); 3, Bendell (1955*c*); 4, Beer (1944); 5, Schotellius (1951*b*).

[b] 23 yearlings and adults ranged from 1 to 5 per individual, 11 juveniles from 1 to 2.

[c] All in juveniles; none was found in yearlings or adults.

[d] One worm only per individual among 14 infected yearlings and adults and 4 infected juveniles.

20.3.1 Integumentary anomalies

Abnormalities of the skin may be associated with either plumage (see 8.1.4), the skin, or both. Those associated with the skin usually involve tumourlike, wartlike, or scalelike growths, or are associated with wounds.

Superficial wounds and sores are relatively common in blue grouse and are sometimes in the process of healing, sometimes healed, and sometimes overtly infected. The unfeathered brood patch appears especially vulnerable to injury, but a number of other superficial wounds, sores, and deeper wounds have been noted. A few abnormalities have been identified that may, or may not, have resulted from injury.

We identified 17 cases of tumours, warts, or other skin disorders that do not appear to have resulted from wounds and were likely innate or related to pathogens (Appendix 2). This is an incidence of 0.2% among the birds examined. Among 16 birds with such disorders and for which body mass was recorded, 14 were normal and 2 subnormal in terms of mass. Twenty-four integumentary injuries (21 superficial) were identified, an incidence of 0.2%, and most had normal body mass. These kinds of afflictions do not appear particularly debilitating and likely are not a serious problem at the population level.

20.3.2 Skeletal anomalies

Skeletal abnormalities may reflect missing or deformed bone associated with birth defects, disease, or injuries.

We recorded 12 skeletal anomalies (Appendix 2) that might have been innate in our sample of birds, an incidence of 0.1%. Among these birds, four were subnormal in terms of body mass, two of which were small chicks (1 and 7 days of age) that likely would not have survived. The most common and likely innate anomaly was missing toes and (or) claws ($n = 8$ birds). Body masses of these birds were usually normal, suggesting little debilitation. Seven skeletal injuries were identified among the birds examined, an incidence of 0.1%, and most of these birds had normal body mass. Skeletal disorders of a debilitating nature are likely of such a low incidence to be unimportant at the population level.

Two individual cases stand out as of special note. One adult female had no manus or primaries on one wing and could not fly, but appeared healthy in other respects. If this was an innate disorder, she had survived flightless to at least 2 years of age and, according to her behaviour and presence of a brood patch, probably had successfully bred in the year found. Survival to this age with such a disability is likely rare. One male, at 8 years of age, was on territory and singing on 31 May, even though lame in one foot. He was still on territory, and singing 3 1/2 weeks later, at which time he was recaptured. His left foot was gone (presumably having dropped off) and body mass was subnormal. Both birds appear to have bred, or attempted to breed, despite severe disabilities. For further detail on these birds see band numbers 12699 and 4148 in Appendix 2.

20.3.3 Summary of anomalies

The total number of birds identified with an abnormality, 64, provides an incidence of 0.6% among birds examined. Of these disorders, 29 (0.3%) may have been innate or disease-related, 31 (0.3%) likely resulted from injuries, and 4 (0.04%) were of miscellaneous, unknown origins. Few showed signs of severe debilitation as indicated by subnormal body mass.

20.4 Synthesis

Few viral, bacterial, or fungal diseases, or instances of same, have been identified in wild blue grouse, more in birds held in captivity. Most of those in aviary birds were enteric or pulmonary disorders and likely caused by aviary conditions or contamination with pathogens of domestic galliforms.

Eleven species of ectoparasites have been found on blue grouse, most of which also occur on other tetraonines. None has been implicated as a serious pathogen in this bird, but work with these parasites has been limited.

Haemoprotists have received the most attention by those studying blue grouse. Four genera and one unidentified microfilaria have been identified. Except *Plasmodium*, all are found at most sites sampled, and apparent absence from some regions may reflect small samples or absence of suitable vectors. Rates and intensities of infection with haemoprotists are often high, but pathological effects have not been detected.

At least 17 helminths (other than microfilariae) have been identified in blue grouse. Prevalence levels are often high, and most species also occur in other tetraonines. Among all species reported, *D. nasuta*, *Rhabdometra odious*, *R. nullicollis*, and *P. formosus* appear to have the greatest potential for causing serious pathologies in wild birds. *D. nasuta* and *P. formosus* have been reported in blue grouse only from Vancouver Island.

A number of physical anomalies have been noted in >10 000 birds handled by us, but the incidence was low, ~0.6%. In most cases these were minor and did not appear to have serious debilitating effects on individuals.

By our definition, disease is any abnormal condition caused by presumed pathogenic organisms. Some such organisms may be more benign than pathogenic under normal circumstances and may cause problems of consequence to the host only under conditions of stress, e.g., food shortage or climatic extremes. Generally, parasites and viral, bacterial, and fungal diseases do not appear to be significant agents of mortality at the population level. We know nothing about possible indirect effects on such things as behaviour, longevity, and reproduction, however, or whether disease might be a barrier to occupation of otherwise suitable habitats. These questions beg for attention. Also, more study is needed in regions that have not been adequately surveyed.

Endnotes [Chapter 20]

1. Campbell River collections include some birds taken at Lower Quinsam.

2. We use body mass as an index to whether an abnormality might be having a deleterious effect on a bird. If mass is within the general range for a bird of a given sex and age class, it is considered normal, if less than the general range, subnormal. We do not include incidences in which birds were struck by vehicles, in which injuries were likely a result of our activities (two exceptions), or cases of minor feather loss.

Postscript

This book is based in large part on our studies at Lower and Middle Quinsam, Comox Burn, and Hardwicke Island, supplemented by other studies on Vancouver and nearby islands. That is because *D.o. fuliginosus* on the central coast has received the most intense and long-term research attention. The strong focus on one coastal subspecies is unfortunate in some ways because most blue grouse inhabit interior regions and because there are a number of clear differences between coastal and interior birds. Concentrated effort on one group, however, has provided a more in-depth view of these particular birds than if studies had been spread more widely. This furnishes a stronger baseline to which other populations can be compared.

There have been many shorter term, intensive investigations of blue grouse in interior regions over the last 6–7 decades, ranging from Alberta and British Columbia in the north to Colorado and California in the south. They have contributed much to our understanding at the species level. We also broadened our own view of the species by visiting other areas and conducting short-term research outside British Columbia. Collectively, these studies have provided much information for comparing across subspecies. Although there are differences between coastal and interior birds, and between populations within regions, there are also many similarities. Recognition of the similarities and differences contributes to our understanding of this bird, a principal objective of this book. From this, we believe some important broad generalizations can be made that seem important in considering further work with this species.

We think blue grouse evolved from within the prairie grouse line in the southern Rocky Mountain region. Their speciation was most likely related to Plio–Pleistocene climatic oscillations and their associated fragmentation and consolidation of regions and biotic communities. This is consistent with Drovetski's (2003) suggestions for speciation events among the Tetraoninae in general, and with recent molecular evidence. Subspeciation likely resulted from similar phenomena.

At the species level, blue grouse have adapted to many different breeding season environments, from sea level to subalpine, mesic and cool to xeric and hot, and old-growth forest to clear-cuts and shrub-steppe high desert. A common denominator to all breeding areas is that they are within the range of mobility of this bird to montane or temperate coniferous forests within which they winter. Such forests appear necessary because conifers provide the great bulk of the bird's winter diet. This may reflect speciation from a prairie grouse-like ancestor in a mountain environment.

Morphological, reproductive, behavioural, and other adaptations of blue grouse must relate to their evolutionary history. Some adaptations, more plastic than others, may vary phenotypically with local conditions. Plasticity itself, however, may be genetic (Dobzhansky 1965) and may account for the ability of this grouse to occupy so many varied habitats, even within regions. One aspect of its life history that seems to lack plasticity is a requirement for breeding habitat associated with coniferous forest, a combination found in mountains of the western Nearctic. Here is an important feature of this bird's biology and may explain its rather narrow longitudinal distribution.

As noted elsewhere, this book is principally documentary. Topics considered vary in depth, a reflection of the availability of information and of our own backgrounds. Interpretations and speculations based on the same data often differ among individuals and, unless specified otherwise, views here are ours. Many questions remain.

A future publication will explore the population ecology of blue grouse—its relation to abundance, distribution, and theory. It will draw heavily on information in this volume.

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Appendix 1. Statistical Tests

Chapter 8. Integument

[1] Comparison between *D.o. pallidus* and *D.o. richardsonii* with respect to the number of each with distinct, indistinct, or no tail bands.
G test: $G = 3.94$, df $= 2$, $n = 413$, $p > 0.1$, n.s.

[2] Comparison of mean widths of tail bands of yearling male to yearling female *D.o. pallidus*.
Student's t test: $t = 2.94$, df $= 58$, $p < 0.01$.

[3] Comparison of mean widths of tail bands of adult males to adult females for (a) *D.o. obscurus*, (b) *D.o. pallidus*, (c) *D.o. richardsonii*, (d) *D.o. howardi*, (e) *D.o. sierrae*, (f) *D.o. fuliginosus*, and (g) *D.o. sitkensis*.
(a–g) Student's t tests: all t values between 3.25 and 8.06, all df between 31 and 118, all p values between 0.01 and <0.001.

[4] Comparison of mean widths of tail bands of adult male to yearling male *D.o. pallidus*.
Student's t test: $t = 2.20$, df $= 83$, $p < 0.03$.

[5] Comparison of mean widths of tail bands of adult females to yearling females for (a) *D.o. pallidus*, (b) *D.o. richardsonii*, (c) *D.o. fuliginosus*, and (d) *D.o. sitkensis*.
(a) Student's t test: $t = 1.81$, df $= 93$, $0.10 > p > 0.05$.
(b–d) Student's t tests: all t values between 0.77 and 1.50, all df between 25 and 47, all p values between >0.13 and 0.54, all n.s.

[6] Comparison of mean widths of tail bands of adult males among subspecies for (a) *D.o. pallidus* × *D.o. richardsonii*, (b) *D.o. pallidus* + *D.o. richardsonii* × *D.o. obscurus*, (c) *D.o. sierrae* × *D.o. fuliginosus* × *D.o. sitkensis*, and (d) *D.o. sierrae* + *D.o. fuliginosus* + *D.o. sitkensis* × *D.o. howardi*.
(a) Student's t test: $t = 0.39$, df $= 91$, $p > 0.69$, n.s.
(b) Student's t test: $t = -19.12$, df $= 128$, $p < 0.001$.
(c) ANOVA: $F_{2,71} = 0.93$, $p > 0.59$, n.s.
(d) Student's t test: $t = -7.69$, df $= 95$, $p < 0.001$.

[7] Comparison of mean widths of tail bands of yearling females among subspecies for (a) *D.o. pallidus* × *D.o. richardsonii* and (b) *D.o. fuliginosus* × *D.o. sitkensis*.
(a) Student's t test: $t = 2.27$, df $= 50$, $p < 0.03$.
(b) Student's t test: $t = -0.49$, df $= 20$, $p > 0.64$, n.s.

[8] Comparison of mean widths of tail bands of adult females between or among subspecies for (a) *D.o. obscurus* × *D.o. pallidus*, (b) *D.o. obscurus* × *D.o. richardsonii*, (c) *D.o. pallidus* × *D.o. richardsonii*, (d) *D.o. sierrae* × *D.o. fuliginosus*, (e) *D.o. sierrae* + *D.o. fuliginosus* × *D.o. howardi*, (f) *D.o. sierrae* + *D.o. fuliginosus* × *D.o. sitkensis*.
(a–c) Student's t tests: all t values between 3.01 and 9.68, all df between 53 and 90, all p values between <0.01 and 0.001.
(d) Student's t test: $t = 0.77$, df $= 50$, $p > 0.54$, n.s.
(e, f) Student's t tests: $t = 4.03$ and 2.58, df $= 60$ and 67, $p < 0.001$ and < 0.02.

[9] Comparison of mean widths of tail bands of adult males between interior and coastal subspecies at generally similar latitudes for (a) *D.o. obscurus* × *D.o. howardi*, (b) *D.o. pallidus* + *D.o. richardsonii* × *D.o. sierrae* + *D.o. fuliginosus* + *D.o. sitkensis*.
(a, b) Student's t tests: $t = 12.64$ and 8.07, df $= 58$ and 165, both p values <0.001.

[10] Comparison of mean widths of tail bands of adult females between interior and coastal subspecies at generally similar latitudes for (a) *D.o. obscurus* × *D.o. howardi*, (b) *D.o. pallidus* × *D.o. sierrae* + *D.o. fuliginosus*, (c) *D.o. richardsonii* × *D.o. sierrae* + *D.o. fuliginosus*, (d) *D.o. pallidus* × *D.o. sitkensis*, and (e) *D.o. richardsonii* × *D.o. sitkensis*.
(a–e) Student's t tests: all t values between 2.98 and 6.97, all df between 27 and 106, all p values between <0.01 and <0.001.

[11] Comparison of mean widths of tail bands between northern interior subspecies and *D.o. howardi* for (a) adult male *D.o. pallidus* + *D.o. richardsonii* × *D.o. howardi*, (b) adult female *D.o. pallidus* × *D.o. howardi*, and (c) adult female *D.o. richardsonii* × *D.o. howardi*.
(a) Student's t test: $t = 2.27$, df $= 114$, $p < 0.03$.
(b, c) Student's t tests: $t = -0.34$ and 1.51, df $= 64$ and 44, $p > 0.73$ and > 0.13, both n.s.

[12] Regressions of primary moult scores on date for birds at Hudson Bay Mt. for (a) adult males and (b) brood females.
(a) $y = -165.388 + 1.002x$; $F_{1,5} = 45.2$, $R = 0.95$, $p < 0.01$.
(b) $y = 612.689 - 6.649x$; $F_{2,18} = 8.59$, $R = 0.70$, $p < 0.01$.

Chapter 9. Morphology

[1] Comparison of mean monthly body masses of adult males at Comox Burn among months for (a) March to August, and (b) March to July.
(a) ANOVA: $F_{5,482} = 2.51$, $p < 0.03$.
(b) ANOVA: $F_{4,477} = 1.91$, $p > 0.10$, n.s.

[2] Comparison of mean monthly body masses of yearling males at Comox Burn among the months April to July.
ANOVA: $F_{3,233} = 0.63$, $p > 0.59$, n.s.

[3] Comparison of mean monthly body masses of yearling lone females between (a) April and May, (b) May and June, (c) June and July, and (d) July and August; and of adult lone females between (e) April and May, (f) May and June, (g) June and July, and (h) July and August, all at Comox Burn.
(a–c) Student's t tests: all t values between -3.38 and -4.71, all df between 68 and 212, all p values between 0.01 and 0.001.
(d) Student's t test: $t = 1.77$, df $= 29$, $0.10 > p > 0.05$, n.s.
(e–g) Student's t tests: all t values between 2.91 and 4.04, all df between 49 and 129, all p values between 0.01 and 0.001.
(h) Student's t test: $t = -0.51$, df $= 18$, $p > 0.62$, n.s.

[4] Comparison of mean monthly body masses of yearling brood females between (a) June and July, and (b) July and August; and of adult brood females between (c) June and July, (d) July and August, and (e) June and August, all at Comox Burn.
(a, b) Student's t tests: $t = 2.53$ and 2.74, df $= 152$ and 177, $p < 0.02$ and < 0.01.
(c, d) Student's t tests: $t = 1.91$ and 0.83, df $= 253$ and 221, $p = 0.054$ and 0.59, n.s.
(e) Student's t test: $t = 2.39$, df $= 162$, $p < 0.02$.

[5] Comparison of (a) mean monthly body masses of adult males at Sheep River among the months May to August; and (b) the grand spring–summer mean mass at Sheep River to that at Comox Burn.
(a) ANOVA: $F_{3,64} = 0.94$, $p > 0.57$, n.s.
(b) Student's t test: $t = 5.20$, df $= 548$, $p < 0.001$.

[6] Comparison of mean monthly body masses of yearling males at Sheep River (a) among the months May to July and (b) between May and July.

(a) ANOVA: $F_{2,23} = 5.64$, $p < 0.02$.

(b) Student's *t* test: $t = -3.28$, df = 13, $p < 0.01$.

[7] Comparison of mean monthly body masses of yearling males at Sheep River in (a) May, (b) June, and (c) July, to the grand spring–summer mean of yearling males at Comox Burn.

(a, b) Student's *t* tests: $t = -5.45$ and -3.29, df = 245 and 247, $p < 0.001$ and < 0.01.

(c) Student's *t* test: $t = -0.43$, df = 242, $p > 0.66$, n.s.

[8] Comparison of mean monthly body masses of adult females at Sheep River between (a) May and June and (b) June–July and August.

(a, b) Student's *t* tests: $t = 6.20$ and -4.08, df = 48 and 89, both p values <0.001.

[9] Comparison of mean monthly body masses of yearling females at Sheep River among the months May to August.

ANOVA: $F_{3,62} = 1.88$, $p > 0.14$, n.s.

[10] Comparison of mean spring–summer body masses of adult males between Comox Burn and (a) Skalkaho, (b) Sheep River, (c) CA–OR–WA, and (d) the Methow Valley; and between Skalkaho and (e) Sheep River, (f) CA–OR–WA, and (g) the Methow Valley.

(a) Student's *t* test: $t = 0.13$, df = 509, $p > 0.88$, n.s.

(b–g) Student's *t* tests: all *t* values between 2.51 and 765, all df between 46 and 548, all p values between <0.02 and <0.001.

[11] Comparison of grand mean spring–summer body masses of adult males between (a) Sheep River and CA–OR–WA, (b) Sheep River and the Methow Valley, and (c) CA–OR–WA and the Methow Valley.

(a) Student's *t* test: $t = 0.00$, df = 85, $p > 0.99$, n.s.

(b, c) Student's *t* tests: $t = 1.98$ and -2.85, df = 107 and 58, $p < 0.01$ and 0.05.

[12] Comparison of mean lengths of (a) body, (b) wing, (c) tail, (d) culmen, (e) foot, (f) tibiotarsus, (g) middle toe, and (h) middle claw (adults only) between yearling males and females (a–g), and between adult males and females (h–q); and (r) of middle claw between yearling males and females.

(a–q) Student's *t* tests: all *t* values between 5.31 and 95.50, all df between 87 and 1004, all p values <0.001.

(r) Student's *t* test: $t = 0.82$, df = 128, $p > 0.58$, n.s.

[13] Comparison of mean lengths of (a) body, (b) wing, (c) tail, (d) culmen, and (e) foot between yearling and adult males (a–e), and between yearling and adult females (f–j); and of (k) tibiotarsus, (l) middle toe, and (m) middle claw between yearling and adult males (k–m) and of (n) tibiotarsus, (o) middle toe, and (p) middle claw between yearling and adult females (n–p).

(a–j) Student's *t* tests: all *t* values between 2.02 and 9.79, all df between 146 and 1081, all p values between 0.04 and <0.001.

(k–p) Student's *t* tests: all *t* values between 0.08 and 1.76, all df between 119 and 210, all p values between 0.08 and >0.92, n.s.

[14] Relationship between body mass and length of foot at Comox Burn for (a) yearling males and (b) adult males.

(a) $y = 78.968$; $F_{1,331} = 52.26$, $R = 0.37$, $p < 0.001$

(b) $y = 77.239$; $F_{1,323} = 50.60$, $R = 0.37$, $p < 0.001$

[15] Relationship between body mass and length of wing at Hardwicke Island for (a) yearling males and (b) adult males.

(a) $y = 192.457$; $F_{1,117} = 12.04$, $R = 0.31$, $p < 0.001$

(b) $y = 191.301$; $F_{1,256} = 32.26$, $R = 0.33$, $p < 0.001$

[16] Comparison of (a) monthly mean masses of *pectoralis majors*, *pectoralis minors*, hearts, proventriculi, livers, spleens, and pancreases, and monthly mean lengths of small intestines, colons, and ceca, among months; and (b) mean mass of the gizzard in April to that in May to July, all for yearling males.

(a) ANOVAS: all p values >0.07, n.s.

(b) Student's *t* test: $t = -4.37$, df = 42, $p < 0.001$.

[17] Comparison of monthly mean masses of gizzard linings of yearling males among months.

ANOVA: $F_{3,40} = 0.58$, $p > 0.63$, n.s.

[18] Comparison of (a) monthly mean masses of *pectoralis majors*, *pectoralis minors*, hearts, livers, and pancreases, and mean lengths of small intestines and ceca, among months; (b) mean mass of the proventriculus in April and May to that in June, (c) mean mass of the proventriculus in June to that in July and August, (d) mean mass of the spleen in April to that in May, (e) mean mass of the spleen in May to that in June to August, and (f) mean mass of the colon in April to that in May to August, all for adult males.

(a) ANOVAS: all p values >0.05, n.s.

(b–f) Student's *t* tests: all *t* values between 2.23 and 3.88, all df between 39 and 103, all p values between <0.03 to <0.01.

[19] Comparison of mean mass of the gizzard of adult males between (a) April and May to June, and (b) May to June and July to August.

(a, b) Student's *t* tests: $t = 7.49$ and -3.52, df 54 and 52, $p < 0.001$ and 0.01.

[20] Comparison of monthly mean masses of gizzard linings of adult males among months.

ANOVA: $F_{4,106} = 1.64$, $p > 0.16$, n.s.

[21] Comparison of (a) monthly mean masses of *pectoralis minors*, proventriculi, spleens, and pancreases, and mean lengths of small intestines, among months; (b) mean mass of the heart in May to July to that in August, (c) mean length of the ceca in April to July to that in August, (d) mean mass of *pectoralis majors* in April and May to that in June to August, (e) mean mass of the gizzard in Aprl and May to that in June to August, (f) mean mass of the liver in April and May to that in June to August, (g) mean length of the colon in May to that in June to August, and (h) mean mass of the gizzard lining in April and May to that in June to August, all for yearling females.

(a) ANOVAS: all p values >0.10, n.s.

(b) ANOVA: $F_{1,70} = 3.20$, $p < 0.03$.

(c) ANOVA: $F_{3,68} = 3.44$, $p < 0.02$.

(d–h) Student's *t* tests: all *t* values between 2.37 and 5.80, all df between 58 and 74, all p values between <0.02 and <0.001.

[22] Comparison of (a) monthly mean masses of proventriculi, and monthly mean lengths of small intestines, among months; (b) mean mass of the heart in April to that in July, (c) mean mass of the gizzard in April to that in June to July, (d) mean length of colon in April to that in June, (e) mean mass of *pectoralis majors* in April and May to that in July and August, (f) mean mass of liver in April and May to that in June to August, (g) mean length of the ceca in April to that in July to August, (h) mean mass of pancreas in April and May to that in June to August, (i) mean mass of *pectoralis minors* in April to June to that in July, (j) mean mass of the spleen in April to June to that in July and August, and (k) mean mass of the gizzard lining in April and May to that in June to August, all for adult females.

(a) ANOVAS: $0.10 > p > 0.05$ and >0.38, both n.s.

(b–k) Student's *t* tests: all *t* values between -3.15 and 10.39, all df between 29 and 1058, all p values between <0.01 and <0.001.

[23] Comparison of mean length of foot of adult males at Hudson Bay Mt. to that of adult males at (a) Hardwicke Island, (b) CA–OR–WA, (c) the Methow Valley, (d) Skalkaho, and (e) Hart's Pass.

(a–e) Student's t tests: all t values between -2.12 and -7.34, all df between 20 and 268, all p values between <0.04 and <0.001.

[24] Comparison of mean length of foot of adult males at Hardwicke Island to that of adult males at (a) Skalkaho, (b) CA–OR–WA, (c) the Methow Valley, (d) Hart's Pass; of adult males at Skalkaho to that of adult males at (e) CA–OR–WA, (f) the Methow Valley, (g) Hart's Pass; and (h) among adult males at CA–OR–WA, the Methow Valley, and Hart's Pass.

(a) Student's t test: $t = 1.66$, df $= 282$, $0.10 > p > 0.05$, n.s.

(b–g) Student's t tests: all t values between -5.62 and 7.67, all df between 34 and 275, all p values <0.001.

(h) ANOVA: $F_{2,42} = 0.80$, $p > 0.54$, n.s.

[25] Relationship between mean body mass and mean length of foot of adult males among populations at Hardwicke Island, Skalkaho, CA–OR–WA, the Methow Valley, Hart's Pass, and Hudson Bay Mt.

$y = 32.580 + 0.053x$; $F_{1,4} = 83.31$, $R = 0.94$, $p < 0.01$.

[26] Comparison of mean length of wing of adult males at Skalkaho to those of adult males at (a) Hardwicke Island, (b) CA–OR–WA, (c) the Methow Valley, (d) Hart's Pass, and (e) Hudson Bay Mt.

(a–e) Student's t tests: all t values between -2.33 and 8.47, all df between 34 and 288, all p values between <0.03 and <0.001.

[27] Comparison of mean length of wing of adult males at the Methow Valley to that at (a) Hardwicke Island, (b) CA–OR–WA, (c) Hart's Pass, and (d) Hudson Bay Mt.

(a–c) Student's t tests: all t values between 2.11 and 4.35, all df between 23 and 277, all p values between <0.05 and <0.001.

(d) Student's t test: $t = 1.62$, df $= 27$, $p < 0.11$, n.s.

[28] Comparison of mean length of wing of adult males at Hardwicke Island to that of adult males at (a) CA–OR–WA, (b) Hudson Bay Mt., and (c) Hart's Pass.

(a, b) Student's t tests: $t = -1.98$ and -2.42, df 274 and 34, $p < 0.05$ and < 0.03.

(c) Student's t test: $t = -1.01$, df $= 270$, $p > 0.31$, n.s.

[29] Relationship between mean body mass and mean length of wing of adult males among populations at Hardwicke Island, Skalkaho, CA–OR–WA, the Methow Valley, Hart's Pass, and Hudson Bay Mt.

$y = 229.25$; $F_{1,4} = 0.005$, $R = 0.055$, $p > 0.92$, n.s.

[30] Comparison of mean length of wing of females at Skalkaho to that at Hardwicke Island for (a) adults and (b) yearlings; and of mean length of foot of females at Skalkaho to that at Hardwicke Island for (c) adults and (d) yearlings.

(a–c) Student's t tests: all t values between -1.47 and 5.86, all df between 361 and 381, all p values between <0.02 and <0.001.

(d) Student's t test: $t = -1.84$, df $= 342$, $0.10 > p > 0.05$, n.s.

[31] Comparison of mean body mass of adult males at Hart's Pass to that at (a) Vancouver–Hardwicke islands, (b) CA–OR–WA, and (c) the Methow Valley.

(a, b) Student's t tests: $t = 5.02$ and 2.29, df $= 126$ and 26, $p < 0.001$ and < 0.03.

(c) Student's t test: $t = 1.187$, df $= 48$, $p > 0.24$, n.s.

[32] Comparison of (a) mean body lengths and (b) mean culmen lengths, of adult males among populations from Vancouver–Hardwicke islands, CA–OR–WA, the Methow Valley, and Hart's Pass.

(a) ANOVA: $F_{3,150} = 1.48$, $p > 0.21$, n.s.

(b) ANOVA: $F_{3,156} = 0.18$, $p > 0.90$, n.s.

[33] Comparison of mean length of tail of adult males at Vancouver–Hardwicke islands to that at (a) CA–OR–WA, (b) the Methow Valley, and (c) Hart's Pass; and (d) among populations at CA–OR–WA, the Methow Valley, and Hart's Pass.

(a–c) Student's t tests: all t values between -3.14 and -4.89, all df between 126 and 133, all p values between <0.01 and <0.001.

(d) ANOVA: $F_{2,42} = 0.16$, $p > 0.21$, n.s.

[34] Comparison of mean length of tibiotarsus of adult males at Vancouver–Hardwicke islands to that at (a) Hart's Pass, (b) CA–OR–WA, and (c) the Methow Valley; and (d) among populations from CA–OR–WA, the Methow Valley, and Hart's Pass.

(a) Student's t test: $t = 2.26$, df $= 94$, $p < 0.03$.

(b) Student's t test: $t = 2.63$, df $= 105$, $0.10 > p > 0.05$.

(c) Student's t test: $t = 1.57$, df $= 101$, $p > 0.11$, n.s.

(d) ANOVA: $F_{2,42} = 0.86$, $p > 0.56$, n.s.

[35] Comparison of mean length of middle toe of adult males at Vancouver–Hardwicke islands to those at (a) CA–OR–WA, (b) the Methow Valley, and (c) Hart's Pass; and (d) among populations at CA–OR–WA, the Methow Valley, and Hart's Pass.

(a–c) Student's t tests: all t values between 2.66 and 3.23, all df between 131 and 140, all p values <0.01.

(d) ANOVA: $F_{2,40} = 0.29$, $p > 0.75$, n.s.

[36] Comparison of mean length of middle claw of adult males among populations at Vancouver–Hardwicke islands, CA–OR–WA, the Methow Valley, and Hart's Pass.

ANOVA: $F_{3,168} = 1.21$, $p > 0.30$, n.s.

[37] Comparison of mean mass of *pectoralis majors* of adult males at Vancouver–Hardwicke islands to that at (a) CA–OR–WA, (b) the Methow Valley, and (c) Hart's Pass; that at CA–OR–WA to that at (d) the Methow Valley, and (e) Hart's Pass; and (f) that at the Methow Valley to that at Hart's Pass.

(a–c) Student's t tests: all t values between 3.37 and 5.70, all df between 100 and 112, all p values between <0.01 and <0.001.

(d) Student's t test: $t = 1.64$, df $= 26$, $p > 0.11$, n.s.

(e) Student's t test: $t = 3.03$, df $= 27$, $p < 0.01$.

(f) Student's t test: $t = 1.16$, df $= 15$, $p > 0.26$, n.s.

[38] Comparison of mean mass of *pectoralis minors* of adult males at Vancouver–Hardwicke islands to that at (a) CA–OR–WA, (b) the Methow Valley, and (c) Hart's Pass; that at CA–OR–WA to that at (d) the Methow Valley and (e) Hart's Pass; and (f) that at the Methow Valley to that at Hart's Pass.

(a–c) Student's t tests: all t values between 2.37 and 6.00, all df between 101 and 112, all p values between <0.02 and <0.001.

(d) Student's t test: $t = -0.24$, df $= 26$, $p > 0.81$, n.s.

(e, f) Student's t tests: $t = 2.43$ and 2.42, df $= 27$ and 15, both p values <0.03

[39] Comparison of mean mass of heart of adult males at Vancouver–Hardwicke islands to that at (a) CA–OR–WA, (b) the Methow Valley, and (c) Hart's Pass; and (d) among populations at CA–OR–WA, the Methow Valley, and Hart's Pass.

(a–c) Student's t tests: all t values between 2.10 and 2.65, all df between 115 and 125, all p values between <0.04 and <0.01.

(d) ANOVA: $F_{2,34} = 0.09$, $p > 0.91$, n.s.

[40] Comparison of mean mass of liver of adult males at Vancouver–Hardwicke islands to those at (a) CA–OR–WA; and (b) among

populations at Vancouver–Hardwicke islands, the Methow Valley, and Hart's Pass.

(a) Student's t test: $t = 3.04$, df $= 126$, $p < 0.01$.
(b) ANOVA: $F_{2,123} = 0.71$, $p > 0.50$, n.s.

[41] Comparison of mean mass of spleen of adult males at CA–OR–WA to that at (a) Vancouver–Hardwicke islands, (b) the Methow Valley, and (c) Hart's Pass; and (d) among populations at Vancouver–Hardwicke islands, the Methow Valley, and Hart's Pass.

(a, b) Student's t tests: $t = -4.79$ and 3.27, df $= 39$ and 19, $p < 0.001$ and < 0.01.
(c) Student's t test: $t = 1.95$, df $= 16$, $0.10 > p > 0.05$.
(d) ANOVA: $F_{2,44} = 0.34$, $p > 0.71$, n.s.

[42] Comparison of mean mass of gizzard of adult males at Vancouver–Hardwicke islands to that at (a) the Methow Valley, (b) CA–OR–WA, and (c) Hart's Pass; that at the Methow Valley to that at (d) CA–OR–WA and (e) Hart's Pass; and (f) that at CA–OR–WA to that at Hart's Pass.

(a) Student's t test: $t = 0.22$, df $= 99$, $p > 0.81$, n.s.
(b–e) Student's t tests: all t values between -4.59 and 7.50, all df between 19 and 107, all p values <0.001.
(f) Student's t test: $t = 0.80$, df $= 27$, $p > 0.56$, n.s.

[43] Comparison of mean mass of proventriculus of adult males at Vancouver–Hardwicke islands to that at (a) the Methow Valley, (b) CA–OR–WA, and (c) Hart's Pass; (d) that at the Methow Valley to that at CA–OR–WA; and (e) that at the Methow Valley to that at Hart's Pass.

(a) Student's t test: $t = -1.12$, df $= 64$, $p > 0.27$, n.s.
(b–e) Student's t tests: all t values between -2.82 and 5.19, all df between 19 and 71, all p values between 0.01 and <0.001.

[44] Comparison of mean length of small intestine of adult males at Vancouver–Hardwicke islands to that at (a) CA–OR–WA, (b) the Methow Valley, and (c) Hart's Pass; and (d) among populations at CA–OR–WA, the Methow Valley, and Hart's Pass.

(a) Student's t test: $t = 6.19$, df $= 124$, $p < 0.001$.
(b) Student's t test: $t = 1.76$, df $= 117$, $0.10 > p > 0.05$, n.s.
(c) Student's t test: $t = 5.82$, df $= 114$, $p < 0.001$.
(d) ANOVA: $F_{2,34} = 3.22$, $0.10 > p > 0.05$, n.s.

[45] Comparison of mean length of ceca of adult males at Vancouver–Hardwicke islands to that at (a) CA–OR–WA, (b) the Methow Valley, and (c) Hart's Pass; and (d) among populations at CA–OR–WA, the Methow Valley, and Hart's Pass.

(a–c) Student's t tests: all t values between 2.59 and 4.36, all df between 116 and 125, all p values between <0.02 and <0.001.
(d) ANOVA: $F_{2,35} = 0.14$, $0.10 > p > 0.05$, n.s.

[46] Comparison of mean length of colon of adult males among populations at Vancouver–Hardwicke islands, CA–OR–WA, the Methow Valley, and Hart's Pass.

ANOVA: $F_{3,129} = 2.50$, $0.10 > p > 0.50$, n.s.

[47] Regression of body mass of adult males banded at Comox Burn and Hardwicke Island on age in years.

$y = 1239.942 + 10.806x$; $F_{1,83} = 6.82$, $R = 0.28$, $p < 0.02$.

[48] Comparison of the number of individual adult males that weighed more at second capture (in a subsequent year) and the number that weighed less at second capture, to a ratio of 1:1.

G test: $G = 7.84$, df $= 1$, $n = 34$, $p < 0.01$.

[49] Regression of length of foot of (a) adult males banded at Comox Burn and Hardwicke Island on age in years and (b) adult females banded at Comox Burn and Hardwicke Island on age in years.

(a) $y = 98.059 + 0.555x$; $F_{1,62} = 8.60$, $R = 0.35$, $p < 0.01$.
(b) $y = 90.479 + 0.0833x$; $F_{1,46} = 0.06$, $R = 0.04$, $p > 0.79$, n.s.

[50] Comparison of (a) mean lengths of sternums, (b) mean depths of sternums, and (c) mean lengths of femurs between adult and yearling males; and of (d) mean lengths of sternums, (e) mean depths of sternums, and (f) mean lengths of femurs between adult and yearling females.

(a) Student's t test: $t = -2.56$, df $= 17$, $p < 0.02$.
(b) Student's t test: $t = -1.95$, df $= 17$, $0.10 > p > 0.05$, n.s.
(c) Student's t test: $t = -2.53$, df $= 19$, $p < 0.02$.
(d–f) Student's t tests: all t values between 0.08 and -1.52, all df between 7 and 8, all p values between >0.16 and >0.93, n.s.

[51] Comparison of (a) mean lengths of sternums, (b) mean depths of sternums, and (c) mean lengths of femurs of adults between males and females; and of (d) mean lengths of sternums, (e) mean depths of sternums, and (f) mean lengths of femurs of yearlings between males and females.

(a–f) Student's t tests: all t values between 3.73 and 10.12, all df between 12 and 14, all p values between <0.01 and <0.001.

Chapter 10. Reproduction

[1] Comparison of distribution of time of hatch in Colorado to that at Comox Burn.

G test: $G = 736.63$, df $= 8$, $n = 3304$, $p < 0.001$.

[2] Comparison of mean egg: (a) length, (b) breadth, (c) volume, and (d) fresh mass, of yearling females to those of adult females, Comox Burn and Hardwicke Island (combined).

(a–d) Student's t tests: all t values between 2.16 and 6.10, all df $= 230$, all p values between 0.04 and 0.001.

[3] Comparison of mean egg mass of adult females in coastal British Columbia to that of adult females at (a) the May Ranch, (b) Duck Creek, and (c) Skalkaho.

(a–c) Student's t tests: all t values between 5.16 and 11.82, all df between 157 and 168, all p values <0.001.

[4] Comparison of mean egg mass of adult females at Duck Creek to that of adult females at (a) the May Ranch and (b) Skalkaho.

(a, b) Student's t tests: $t = 5.40$ and 6.36, df $= 29$ and 39, both p values <0.001.

[5] Comparison of mean egg mass of adult females at the May Ranch to that of adult females at Skalkaho.

Student's t test: $t = 1.14$, df $= 40$, $p > 0.25$, n.s.

[6] Comparison of mean shell thickness of eggs among areas for (a) Comox Burn, Hardwicke Island, the May Ranch, the Methow Valley, and Skalkaho and (b) Comox Burn, the May Ranch, the Methow Valley, and Skalkaho.

(a) ANOVA: $F_{5,122} = 2.61$, $p < 0.03$.
(b) ANOVA: $F_{4,95} = 1.95$, $p > 0.1$, n.s.

[7] Comparison of mean shell thickness of eggs from Comox Burn, the May Ranch, the Methow Valley, and Skalkaho (combined) to that of eggs from Hardwicke Island.

Student's t test: $t = 2.72$, df $= 126$, $p < 0.01$.

[8] Comparison of distances between adjacent nests to distances of nests to activity centres of nearest territorial males, Comox Burn. Data extrapolated from Table 2 of Lance (1967).

Mann–Whitney U test: $U = 2.0$, $n_1 = 6$, $n_2 = 7$, $p < 0.001$.

[9] Comparison of nest lining as poor, moderate, or good among nests from Comox Burn, Hardwicke Island, and interior populations.

G test: $G = 0.33$, df $= 4$, $n = 200$, $p > 0.32$, n.s.

[10] Comparison of nest lining as poor, moderate, or good between nests of yearling and adult hens.

G test: $G = 0.80$, df $= 2$, $n = 132$, $p > 0.79$, n.s.

[11] Comparison of nest lining as poor, moderate, or good between nests in the pre- and post-laying periods.
G test: $G = 6.79$, df $= 2$, $n = 202$, $p < 0.03$.

[12] Regression of nest lining as poor, moderate, or good on days after incubation began.
$y = 2.952 - 0.04x$; $F_{1,43} = 6.10$, $R = 0.35$, $p < 0.02$.

[13] Comparison of mean t_e values among sampling periods at (a) Middle Quinsam nest and (b) Comox Burn nest.
(a) ANOVA: $F_{2,260} = 7.99$, $p < 0.01$.
(b) ANOVA: $F_{2,262} = 2.09$, $p > 0.12$, n.s.

[14] Comparison of mean t_n values among sampling periods at (a) Middle Quinsam nest and (b) Comox Burn nest.
(a) ANOVA: $F_{2,260} = 378.5$, $p < 0.001$.
(b) ANOVA: $F_{2,262} = 776.28$, $p < 0.001$.

[15] Regression of mean t_e values for each monitoring period on (a) mean t_a values and (b) mean t_g values for each period, respectively.
(a) $y = 32.505 + 0.084x$; $F_{1,4} = 1.85$, $R = 0.56$, $p > 0.24$, n.s.
(b) $y = 31.938 + 0.113x$; $F_{1,4} = 3.07$, $R = 0.66$, $p > 0.15$, n.s.

[16] Regression of mean t_n values for each monitoring period on (a) mean t_a values and (b) mean t_g values for each period, respectively.
(a) $y = 18.082 + 0.615x$; $F_{1,4} = 20.51$, $R = 0.91$, $p < 0.02$.
(b) $y = 15.883 + 0.744x$; $F_{1,4} = 60.32$, $R = 0.97$, $p < 0.01$.

[17] Comparison of mean distance between first and second nests of individual females within years (renests) to that of first and later nests of individual females between years.
Student's t test: $t = 0.38$, df $= 34$, $p > 0.70$, n.s.

[18] Comparison of mean clutch size of adult to yearling females, Comox Burn, 1969–1978.
Mann–Whitney U test: $U = 794.5$, $n_1 = 73$, $n_2 = 68$, $p < 0.001$.

[19] Comparison of mean clutch sizes among 2-year-old, 3-year-old, and $\geq$4-year-old females at (a) Comox Burn and (b) Hardwicke Island.
(a) ANOVA: $F_{2,941} = 2.45$, $p > 0.13$, n.s.
(b) ANOVA: $F_{2,54} = 1.15$, $p > 0.32$, n.s.

[20] Comparison of mean clutch sizes among years at Comox Burn: data for 1962, 1964, 1969, and 1971–1975. Data for years with samples <10 excluded.
ANOVA: $F_{7,133} = 2.44$, $p < 0.03$.

[21] Comparison of mean clutch sizes of (a) adult females, (b) yearling females, and (c) all females at Hardwicke Island to those at Comox Burn.
(a–c) Student's t tests: all t values between 2.66 and 7.50, all df between 130 and 299, all p values <0.01.

[22] Comparison of mean clutch size of interior females to that of females at Comox Burn.
Mann–Whitney U test: $U = 7022$, $n_1 = 118$, $n_2 = 159$, $p < 0.001$.

[23] Comparison of mean clutch size of presumed first nests to presumed renests for (a) adult females and (b) yearling females.
(a) Student's t test: $t = 5.96$, df $= 68$, $p < 0.001$.
(b) Student's t test: $t = 1.93$, df $= 440$, $0.06 > p > 0.05$, n.s.

[24] Comparison of egg fertility of adult females to that of yearling females at Comox Burn.
G test: $G = 0.88$, df $= 1$, $n = 565$, $p > 0.34$, n.s.

[25] Comparison of egg fertility of females at Comox Burn among the years: (a) 1969–1977 and (b) 1969, 1970, 1972, 1973, 1975–1977.
(a) G test: $G = 19.06$, df $= 8$, $n = 661$, $p < 0.02$.
(b) G test: $G = 8.28$, df $= 6$, $n = 406$, $p > 0.21$, n.s.

[26] Comparison of egg fertility of interior females to that of females at (a) Comox Burn and (b) Hardwicke Island.
(a) G test: $G = 11.35$, df $= 1$, $n = 885$, $p < 0.001$.
(b) G test: $G = 1.91$, df $= 1$, $n = 804$, $p > 0.15$, n.s.

[27] Comparison of egg hatchability of females at Comox Burn among the years: (a) 1969–1977 and (b) 1969, 1970, 1972, 1973, and 1975.
(a) G test: $G = 19.07$, df $= 8$, $n = 621$, $p < 0.02$.
(b) G test: $G = 6.98$, df $= 4$, $n = 232$, $p > 0.13$, n.s.

[28] Comparison of egg hatchability of females at Comox Burn to that at Hardwicke Island.
G test: $G = 19.79$, df $= 1$, $n = 1438$, $p < 0.001$.

[29] Comparison of egg hatchability of interior females to that at (a) Comox Burn and (b) Hardwicke Island.
(a) G test: $G = 9.27$, df $= 1$, $n = 1055$, $p < 0.01$.
(b) G test: $G = 1.15$, df $= 1$, $n = 1098$, $p > 0.28$, n.s.

[30] Comparison of hatchability of fertile eggs of interior females to that at (a) Comox Burn and (b) Hardwicke Island.
(a) G test: $G = 0.01$, df $= 1$, $n = 774$, $p > 0.89$, n.s.
(b) G test: $G = 3.44$, df $= 1$, $n = 698$, $0.06 > p > 0.05$, n.s.

[31] Comparison of general nesting success among years at (a) Comox Burn, 1969–1978, (b) Hardwicke Island, 1979–1984, and (c) Comox Burn: 1969, 1971–1975, and 1977.
(a) G test: $G = 28.97$, df $= 9$, $n = 146$, $p < 0.001$.
(b) G test: $G = 5.90$, df $= 5$, $n = 77$, $p > 0.31$, n.s.
(c) G test: $G = 12.15$, df $= 6$, $n = 126$, $0.1 > p > 0.05$, n.s.

[32] Comparison of general nesting success at Comox Burn to that at Hardwicke Island.
G test: $G = 18.95$, df $= 1$, $n = 223$, $p < 0.001$.

[33] Comparison of general nesting success at Ash River to that at (a) Comox Burn and (b) Hardwicke Island.
(a) G test: $G = 1.52$, df $= 1$, $n = 196$, $p > 0.21$, n.s.
(b) G test: $G = 5.57$, df $= 1$, $n = 127$, $p < 0.02$, n.s.

[34] Comparison of general nesting success of interior females: (a) among populations at Sheep River, Methow River, Green Mt., and Skalkaho; and that of composite interior sample to females at (b) Comox Burn and (c) Hardwicke Island.
(a) G test: $G = 1.44$, df $= 4$, $n = 86$, $p > 0.84$, n.s.
(b) G test: $G = 6.34$, df $= 1$, $n = 232$, $p < 0.02$.
(c) G test: $G = 3.27$, df $= 1$, $n = 163$, $0.08 > p > 0.05$, n.s.

Chapter 11. Growth and Development

[1] Comparison of body masses of day-old chicks at Comox Burn to a normal distribution.
Kolmogorov–Smirnov one-sample test: $D = 0.131$, $n = 321$, $p < 0.02$.

[2] Comparison of body mass of newly hatched chicks at Comox Burn to those at (a) the May Ranch, (b) the Methow Valley, (c) Skalkaho, and (d) Duck Creek.
(a–d) Student's t tests: all t values between 4.22 and 15.48, all df between 331 and 362, all p values between <0.01 and <0.001.

[3] Comparison of mean body mass of newly hatched chicks at Duck Creek to that at (a) Skalkaho and (b) the Methow Valley.
(a, b) Student's t tests: $t = 6.44$ and -4.58, df $= 54$ and 25, both p values <0.001.

[4] Comparison of mean body mass of new chicks on day 1 to those on day 2, Comox Burn.
Student's t test: $t = -0.68$, df $= 599$, $p > 0.50$, n.s.

[5] Regression of mean body mass on age of chicks, 1–5 days of age, Comox Burn.

$y = 25.68 - 0.199x + 0.221x^2$; $F_{2,2} = 101.50$, $R = 1.00$, $p < 0.01$.

[6] Comparison of mean body mass of chicks on (a) day 2 to day 3, (b) day 3 to day 4, and (c) day 4 to day 5, Comox Burn.

(a–c) Student's t tests: all t values between −3.56 and 5.55, all df between 294 and 473, all p values between <0.01 and <0.001.

[7] Regression of mean mass of residual yolk on age of chicks, 1–5 days of age, Comox Burn.

$y = 7.72 - 3.980x + 0.665x^2 - 0.034x^3$; $F_{3,1} = 774.9$, $R = 1.00$, $p < 0.03$.

[8] Regressions of mean weekly body mass of (a) male chicks and (b) female chicks, on age, 1–13 weeks of age, Comox Burn.

(a) $y = 23.211 - 0.137x + 8.780x^2 - 0.272x^3$; $F_{3,9} = 1021.9$, $R = 1.00$, $p < 0.001$.

(b) $y = 17.911 - 0.622x + 8.146x^2 - 0.321x^3$; $F_{3,9} = 2793.7$, $R = 1.00$, $p < 0.001$.

[9] Comparison of mean body mass of male to female chicks in week 4, Comox Burn.

Student's t test: $t = 2.30$, df = 13, $p < 0.04$.

[10] Comparison of mean body mass of male to female chicks in weeks (a) 8, (b) 9, (c) 10, (d) 11, (e) 12, and (f) 13, Comox Burn.

(a–f) Student's t tests: all t values between 5.51 and 15.85, all df between 24 and 326, all p values <0.001.

[11] Comparison of mean body mass of 1- and 2-day-old (combined) male chicks to female chicks, Comox Burn.

Student's t test: $t = 1.75$, df = 72, $0.10 > p > 0.05$, n.s.

[12] Regressions of mean weekly gains in body mass of (a) male chicks and (b) female chicks, on age, 1–13 weeks of age, Comox Burn.

(a) $y = -15.348 + 21.294x - 1.056x^2$; $F_{2,9} = 3.633$, $R = 0.67$, $0.10 > p > 0.05$, n.s.

(b) $y = -19.010 + 21.112x - 1.238x^2$; $F_{2,9} = 9.369$, $R = 0.82$, $p < 0.01$.

[13] Regressions of weekly percentage change in body mass of (a) male chicks and (b) female chicks, on age, 1–13 weeks of age, Comox Burn.

(a) $y = 85.455 - 6.625x$; $F_{1,10} = 12.204$, $R = 0.74$, $p < 0.01$.

(b) $y = 75.432 - 5.816x$; $F_{1,10} = 43.899$, $R = 0.90$, $p < 0.001$.

[14] Regressions of mean weekly body masses of (a) chicks, sex unknown, (b) male chicks, and (c) female chicks, on age, 1–15 weeks of age, westcentral Montana.

(a) $y = 31.732 - 4.685x + 10.744x^2$; $F_{2,5} = 1965.8$, $R = 1.00$, $p < 0.001$.

(b) $y = -586.9 + 219.386x - 7.144x^2$; $F_{2,7} = 295.38$, $R = 0.99$, $p < 0.001$.

(c) $y = -405.859 + 169.173x - 5.625x^2$; $F_{2,7} = 130.29$, $R = 0.99$, $p < 0.001$.

[15] Regressions of mean weekly length of foot of male and female chicks: (a) on age, 1–13 weeks of age, and (b) relationship between foot and body mass, Comox Burn.

(a) males: $y = 36.583 + 7.054x + 0.294x^2 - 0.038x^3$; $F_{3,7} = 286.18$, $R = 1.00$, $p < 0.001$.

females: $y = 39.420 + 3.746x + 0.727x^2 - 0.057x^3$; $F_{3,7} = 666.9$, $R = 1.00$, $p < 0.001$.

(b) males: $y = 41.392 + 0.182x$; $F_{2,8} = 685.3$, $R = 1.00$, $p < 0.001$.

females: $y = 40.402 + 0.185x$; $F_{2,8} = 2566.7$, $R = 1.00$, $p < 0.001$.

[16] Regressions of mean length of wing of male and female chicks on (a) age, 1–13 weeks of age, and (b) relationship between wing and body mass, Hardwicke Island.

(a) males: $y = 13.885 + 29.811x - 1.320x^2$; $F_{3,9} = 1671.0$, $R = 1.00$, $p < 0.001$.

females: $y = 11.822 + 33.565x - 2.11x^2 + 0.046x^3$; $F_{3,9} = 1104.3$, $R = 1.00$, $p < 0.001$.

(b) males: $y = 37.361 + 0.658x$; $F_{3,9} = 317.4$, $R = 1.00$, $p < 0.001$.

females: $y = 32.187 + 0.782x$; $F_{3,9} = 241.2$, $R = 0.99$, $p < 0.001$.

[17] Regressions of mass of *pectoralis major* and *pectoralis minor* muscles of (a) male chicks and (b) female chicks, on age in days, data for Comox Burn and Hardwicke Island combined.

(a) *p major*: $y = 2.211 - 0.5225x + 0.0465x^2 - 0.0003x^3$; $F_{3,57} = 551.2$, $R = 0.98$, $p < 0.001$.

p minor: $y = 0.5047 - 0.1102x + 0.0111x^2$; $F_{3,59} = 800.6$, $R = 0.99$, $p < 0.001$.

(b) *p major*: $y = 0.4154 - 0.0382x + 0.017x^2$; $F_{3,46} = 926.6$, $R = 0.99$, $p < 0.001$.

p minor: $y = 0.0757 - 0.013x + 0.0058x^2$; $F_{3,46} = 614.4$, $R = 0.99$, $p < 0.001$.

[18] Relationship between masses of *pectoralis major* and *pectoralis minor* muscles and body masses of (a) male chicks and (b) female chicks, data for Comox Burn and Hardwicke Island combined.

(a) *p major*: $y = -3.612 + 0.141x$; $F_{1,59} = 2541.3$, $R = 0.99$, $p < 0.001$.

p minor: $y = -1.360 + 0.047x$; $F_{1,61} = 4501.5$, $R = 0.99$, $p < 0.001$.

(b) *p major*: $y = -4.080 + 0.146x$; $F_{1,44} = 1564.3$, $R = 0.99$, $p < 0.001$.

p minor: $y = -1.335 - 0.046x$; $F_{1,43} = 3294.2$, $R = 0.99$, $p < 0.001$.

[19] Regressions of mass of hearts of male and female chicks on (a) age in days and (b) relationships between mass of hearts of male and female chicks and body mass, data for Comox Burn and Hardwicke Island combined.

(a) male: $y = 0.027 + 0.029x + 0.0004x^2$; $F_{2,72} = 327.33$, $R = 0.95$, $p < 0.001$.

female: $y = -0.028 + 0.043x + 0.000074x^2$; $F_{2,59} = 223.15$, $R = 0.94$, $p < 0.001$.

(b) male: $y = 0.079 + 0.006x$; $F_{1,73} = 954.5$, $R = 0.96$, $p < 0.001$.

female: $y = 0.049 + 0.007x$; $F_{1,54} = 722.5$, $R = 0.96$, $p < 0.001$.

[20] Regressions of mass of livers of male and female chicks on (a) age in days and (b) relationships between mass of livers of male and female chicks and body mass, data for Comox Burn and Hardwicke Island combined.

(a) male: $y = 0.559 + 0.056x + 0.004x^2$; $F_{2,70} = 536.17$, $R = 0.97$, $p < 0.001$.

female: $y = 0.569 + 0.073x + 0.003x^2$; $F_{2,57} = 453.30$, $R = 0.97$, $p < 0.001$.

(b) male: $y = 0.005 + 0.034x$; $F_{1,70} = 1396.3$, $R = 0.98$, $p < 0.001$.

female: $y = 0.108 + 0.035x$; $F_{1,54} = 799.8$, $R = 0.97$, $p < 0.001$.

[21] Regressions of mass of gizzards of male and female chicks on (a) age in days and (b) relationships between mass of gizzards of male and female chicks and body mass, data for Comox Burn and Hardwicke Island combined.

(a) male: $y = 0.235 + 0.169x + 0.002x^2$; $F_{2,70} = 1401.0$, $R = 0.99$, $p < 0.001$.
female: $y = 0.391 + 0.170x + 0.002x^2$; $F_{2,58} = 1069.0$, $R = 0.99$, $p < 0.001$.
(b) male: $y = 0.563 + 0.035x$; $F_{1,71} = 4018.0$, $R = 0.99$, $p < 0.001$.
female: $y = 0.804 + 0.035x$; $F_{1,53} = 1380.2$, $R = 0.98$, $p < 0.001$.

[22] Regressions of length of small intestines of male and female chicks on (a) age in days and (b) relationships between length of small intestines of male and female chicks and body mass, data for Comox Burn and Hardwicke Island combined.
(a) male: $y = 285.439 + 28.461x$; $F_{2,53} = 217.7$, $R = 0.94$, $p < 0.001$.
female: $y = 262.031 + 25.762x$; $F_{2,52} = 274.7$, $R = 0.96$, $p < 0.001$.
(b) male: $y = 394.334 + 3.363x$; $F_{2,52} = 143.5$, $R = 0.92$, $p < 0.001$.
female: $y = 314.151 + 4.157x$; $F_{2,48} = 168.7$, $R = 0.94$, $p < 0.001$.

[23] Regressions of length of ceca of male and female chicks on (a) age in days and (b) relationships between length of ceca of male and female chicks and body mass, data for Comox Burn and Hardwicke Island combined.
(a) male: $y = 88.963 + 8.518x$; $F_{2,56} = 411.6$, $R = 0.97$ $p < 0.001$.
female: $y = 89.285 + 7.171x$; $F_{2,53} = 247.5$, $R = 0.95$, $p < 0.001$.
(b) male: $y = 118.555 + 1.127x$; $F_{2,55} = 275.3$, $R = 0.95$, $p < 0.001$.
female: $y = 108.173 + 1.052x$; $F_{2,49} = 172.3$, $R = 0.94$, $p < 0.001$.

[24] Regressions of length of colon of male and female chicks on (a) age in days and (b) relationships between length of colon of male and female chicks and body mass, data for Comox Burn and Hardwicke Island combined.
(a) male: $y = 38.922 + 1.708x$; $F_{2,55} = 163.9$, $R = 0.93$, $p < 0.001$.
female: $y = 31.722 + 2.229x$; $F_{2,54} = 220.4$, $R = 0.94$, $p < 0.001$.
(b) male: $y = 44.555 + 0.229x$; $F_{2,54} = 124.4$, $R = 0.91$, $p < 0.001$.
female: $y = 37.202 + 0.330x$; $F_{2,50} = 126.9$, $R = 0.91$, $p < 0.001$.

Chapter 12. Food, Nutrition, Grit, Water, and Excretion

[1] Comparison of numbers of feeding pecks at the ground to numbers of pecks at plants between chicks ≤ 2 weeks of age and those 2–4 weeks of age.
G test: $G = 83.90$, df = 1, $n = 1555$, $p < 0.001$.

[2] Comparison of distances of nests from water between coast forest and interior Washington.
Student's t test: $t = -6.94$, df = 457, $p < 0.001$.

[3] Comparison of general nesting success between females in coast forest and interior Washington.
G test: $G = 0.069$, df = 1, $n = 237$, n.s.

[4] Regression of (a) mass of gizzard stones and (b) number of gizzard stones, on age of chicks; data from Lower Quinsam, Middle Quinsam, and Comox Burn combined.
(a) $y = -0.466 + 0.153x - 0.007x^2$; $F_{3,45} = 51.18$, $R = 0.88$, $p < 0.001$.
(b) $y = 16.906 + 10.283x - 0.431x^2$; $F_{3,31} = 11.65$, $R = 0.71$, $p < 0.001$.

[5] Comparison of grit mass of adult males at Lower and Middle Quinsam to that of (a) yearling males, (b) adult females, and (c) yearling females.
(a) Student's t test: $t = 2.60$, df = 131, $p < 0.01$.
(b) Student's t test: $t = 1.64$, df = 122, $0.1 > p > 0.05$, n.s.
(c) Student's t test: $t = 2.59$, df = 117, $p < 0.02$.

[6] Comparison of grit volume of adult males at Lower and Middle Quinsam to that of (a) yearling males, (b) adult females, and (c) yearling females.
(a) Student's t test: $t = 2.66$, df = 131, $p < 0.01$.
(b) Student's t test: $t = 1.80$, df = 122, $0.1 > p > 0.05$, n.s.
(c) Student's t test: $t = 2.67$, df = 117, $p < 0.01$.

[7] Comparison of grit mass of yearling males at Lower and Middle Quinsam to that of (a) adult females and (b) yearling females, and (c) of adult females to that of yearling females.
(a–c) Student's t tests: all t values between -0.60 and 1.08, all df between 35 and 49, all p values between 0.29 and 0.56, all n.s.

[8] Comparison of grit volume of yearling males at Lower and Middle Quinsam to that of (a) adult females and (b) yearling females; and (c) that of adult females to that of yearling females.
(a–c) Student's t tests: all t values between -0.45 and 1.00, all df between 35 and 49, all p values between 0.62 and 0.66, all n.s.

[9] Comparison of grit mass of adult males at Comox Burn to that of (a) yearling males, (b) adult females, and (c) yearling females.
(a) Student's t test: $t = 0.75$, df = 60, $p = 0.54$., n.s.
(b, c) Student's t tests: $t = 2.47$ and 4.66, df = 76 and 64, $p < 0.02$ and < 0.001.

[10] Comparison of grit mass of yearling males at Comox Burn to that of (a) adult females, (b) yearling females; and (c) of adult females to those of yearling females.
(a) Student's t test: $t = 1.38$, df = 52, $p = 0.17$, n.s.
(b) Student's t test: $t = 3.73$, df = 40, $p < 0.01$.
(c) Student's t test: $t = 1.19$, df = 56, $p > 0.23$, n.s.

[11] Regression of grit mass of (a) yearling plus adult males on date and (b) yearling plus adult females on date, combined data from lowland and subalpine Vancouver Island.
(a) $y = 13.001 - 0.059x$; $F_{2,192} = 27.02$, $R = 0.47$, $p < 0.001$.
(b) $y = 12.470 - 0.026x$; $F_{1,93} = 18.99$, $R = 0.41$, $p < 0.001$.

[12] Regression of grit volume of (a) yearling plus adult males on date and (b) yearling plus adult females on date, combined data from lowland and subalpine Vancouver Island.
(a) $y = 4.834 - 0.021x$; $F_{2,130} = 18.77$, $R = 0.47$, $p < 0.001$.
(b) $y = 5.104 - 0.010x$; $F_{1,35} = 10.20$, $R = 0.47$, $p < 0.01$.

[13] Regression of grit mass of (a) adult plus yearling males on body mass and (b) adult plus yearling females on body mass, combined data from lowland and subalpine Vancouver Island.
(a) $y = 4.736$; $F_{1,56} = 9.10$, $R = 0.24$, $0.10 > p > 0.05$, n.s.
(b) $y = -5.456 + 0.015x$; $F_{1,54} = 39.08$, $R = 0.65$, $p < 0.001$.

Chapter 13. Energetics

[1] Comparison of mean $\bar{n}_b$ of (a) yearling males to that of adult males, (b) yearling females to that of adult females, (c) adult broodless females to that of adult brood females, and (d) adult plus yearling males to that of adult plus yearling females.

(a) Student's t test: $t = 1.59$, df $= 59$, $p > 0.11$, n.s.
(b) Student's t test: $t = 2.25$, df $= 57$, $p < 0.03$.
(c) Student's t test: $t = -0.63$, df $= 32$, $p > 0.54$, n.s.
(d) Student's t test: $t = 1.42$, df $= 118$, $p > 0.15$ n.s.

[2] Regression of (a) yearling female t_b and (b) adult female t_b on body mass.
(a) $y = 45.295 - 0.00398x$; $F_{1,18} = 6.55$, $R = 0.52$, $p < 0.02$.
(b) $y = 44.650 - 0.00262x$; $F_{1,19} = 7.98$, $R = 0.54$, $p < 0.02$.

[3] Regression of yearling plus adult male t_b on body mass.
ANOVA: $F_{1,55} = 1.70$, $p > 0.19$, n.s.

[4] Comparison of mean t_b of 35–67-day-old chicks to the grand mean t_b of all yearlings and adults.
Student's t test: $t = 1.34$, df $= 130$, $p > 0.17$, n.s.

Chapter 15. Behaviour *per se*

[1] Comparison of numbers of females with broods that flushed out of sight to those of males found hooting that flushed out of sight, Comox Burn, 1971 and 1972.
G test: $G = 66.37$, df $= 1$, $n = 427$, $p < 0.001$.

[2] Comparison of numbers of lone females that flushed out of sight to those of silent males and those found hooting that flushed out of sight, Comox Burn, 1971 and 1972.
G test: $G = 26.30$, df $= 2$, $n = 834$, $p < 0.001$.

[3] Comparison of numbers of lone females that flushed out of sight to those of silent males that flushed out of sight, Comox Burn, 1971 and 1972.
G test: $G = 0.40$, df $= 1$, $n = 603$, $p > 0.52$, n.s.

[4] Comparison of numbers of song types (notes per song) of *D.o. pallidus* males to those of a combined sample of *D.o. sierrae*, *D.o. fuliginosus*, and *D.o. sitkensis* males.
G test: $G = 470.90$, df $= 3$, $n = 694$, $p < 0.001$.

[5] Comparison of numbers of yearling males classified as alone or not alone when first found during the periods: (a) on or before 22 April to 23 April to 1 July and (b) on or before 1 July to on or after 2 July, Hardwicke Island, 1979–1984.
(a) G test: $G = 0.74$, df $= 1$, $n = 144$, $p > 0.39$, n.s.
(b) G test: $G = 8.61$, df $= 1$, $n = 188$, $p < 0.01$.

[6] Comparison of numbers of hooting and silent adult males to hooting and silent yearling males at Middle Quinsam, 1958–1962.
G test: $G = 41.36$, df $= 1$, $n = 279$, $p < 0.001$.

[7] Comparison of numbers of lone females flushed before being seen to that of lone males for the 4-week periods beginning: (a) 16 April, (b) 14 May, (c) 11 June, and (d) on or after 9 July. All at Comox Burn, 1971 and 1972.
(a) G test: $G = 6.666$, df $= 1$, $n = 289$, $p < 0.01$.
(b) G test: $G = 2.82$, df $= 1$, $n = 332$, $0.10 > p > 0.09$, n.s.
(c) G test: $G = 12.20$, df $= 1$, $n = 154$, $p < 0.001$.
(d) G test: $G = 0.93$, df $= 1$, $n = 81$, $p > 0.33$, n.s.

[8] Comparison of number of adult to yearling males that landed on loud wing, Comox Burn, 1971–1972.
G test: $G = 4.03$, df $= 1$, $n = 85$, $p < 0.05$.

[9] Comparison of numbers of lone females that were not seen till flushed among 4-week periods (Fig. 14.1), Comox Burn, 1971 and 1972.
G test: $G = 6.50$, df $= 3$, $n = 248$, $0.10 > p > 0.09$, n.s.

[10] Comparison of numbers of lone females that clucked prior to 9 July to those that clucked after 9 July, Comox Burn, 1971 and 1972.
G test: $G = 8.23$, df $= 3$, $n = 296$, $p < 0.05$.

[11] Comparison of numbers of females present at nests during visits in full daylight hours vs. evening or early morning hours at Lower Quinsam; data from Bendell (1954).
G test: $G = 8.49$, df $= 1$, $n = 49$, $p < 0.01$.

[12] Regressions of (a) mean clucking responses of hens, (b) mean total responses, and (c) mean minimum distances of hens to observers during distraction display, all on ages of chicks, in days; Comox Burn, 1971.
(a) $y = 2.8584 + 0.00903x - 0.00104x^2$; $F_{2,3} = 70.51$, $R = 0.99$, $p < 0.004$.
(b) $y = 2.3379 - 0.0361x$; $F_{1,4} = 35.89$, $R = 0.95$, $p < 0.006$.
(c) $y = 2.7510 - 0.48663x$; $F_{1,4} = 79.95$, $R = 0.98$, $p < 0.003$.

[13] Comparison between Green Mt. and Whiteley Peak in numbers of birds found alone to those found in flocks; data from Cade (1985).
G test: $G = 2.41$, df $= 1$, $n = 155$, $p > 0.12$, n.s.

Chapter 16. Use of Habitat

[1] Comparison of numbers of birds observed in given plant communities to amount of each community at the May Ranch, Duck Creek, Skalkaho, and Hudson Bay Mt.—based on data used to generate Table 16.1.
G tests in all cases; all significant G values at $p < 0.05$.

[2] Comparison of numbers of males singing from the ground, logs, stumps, or trees between (a) 1971–1972 and 1976–1977 at Comox Burn and (b) 1979–1981 and 1982–1984 at Hardwicke Island.
(a) G test: $G = 44.02$, df $= 3$, $n = 498$, $p < 0.001$.
(b) G test: $G = 33.96$, df $= 3$, $n = 1365$, $p < 0.001$.

[3] Comparison of numbers of males singing from the ground or from logs, stumps, and trees in daytime to those singing from the ground or from logs, stumps, and trees in crepuscular hours, Comox Burn, 1971–1973.
G test: $G = 16.83$, df $= 1$, $n = 474$, $p < 0.001$.

Chapter 17. Movements and Use of Space

[1] Comparison of numbers of yearling:adult females killed by hunters to numbers of yearling:adult females on breeding range in spring–summer, 1969–1978, Comox Burn and vicinity.
G test: $G = 33.64$, df $= 1$, $n = 1018$, $p < 0.001$.

[2] Comparison of numbers of juveniles departing from brood ranges per week to a normal distribution, last week of August to third week in November, Hardwicke Island, 1979–1981; data from Fig. 2.4 of Hines (1986*a*).
Kolmogorov–Smirnov 1 sample test: $D = 0.14$, $n = 13$, $p > 0.61$, n.s.

[3] Comparison of distances from point of banding to where grouse were shot by hunters in year marked (direct recoveries) to distances where shot in years beyond those when marked (indirect recoveries), Methow Game Range and vicinity (moves < 1.6 km excluded).
Student's t test: $t = 0.57$, df $= 20$, $p > 0.58$, n.s.

[4] Comparison of distances from point of banding of yearling and adult females to where shot by hunters to those for yearling and adult males, Methow Game Range and vicinity.
Mann–Whitney U test: $U = 2.0$, $n_1 = 3$, $n_2 = 6$, $p < 0.05$.

[5] Comparison of distances moved from breeding range at Comox Burn to where shot by hunters: (a) among the months August,

September, October, and November, (b) between August and September, (c) between October and November, and (d) between August–September and October–November.

(a) ANOVA: $F_{3,28} = 3.47$, $p < 0.03$.

(b, c) Student's t tests: $t = -0.74$ and -0.24, df = 18 and 9, $p > 0.52$ and 0.81, both n.s.

(d) Student's t test: $t = -3.26$, df = 30, $p < 0.01$.

[6] Comparison of distances moved from breeding range at Comox Burn to where shot by hunters between males and females in (a) August–September and (b) October–November.

(a) Student's t test: $t = -0.30$, df = 18, $p > 0.76$, n.s.

(b) Student's t test: $t = 2.64$, df = 9, $p < 0.03$.

[7] Comparison of natal dispersal distances between males and females for (a) yearlings, (b) adults, and (c) yearlings plus adults; Comox Burn and vicinity, 1969–1979.

(a) Mann–Whitney U test: $U = 1497$, $n_1 = 53$, $n_2 = 72$, $p < 0.05$.

(b) Mann–Whitney U test: $U = 1085$, $n_1 = 39$, $n_2 = 77$, $p < 0.02$.

(c) Mann–Whitney U test: $U = 3664$, $n_1 = 80$, $n_2 = 118$, $p < 0.01$.

[8] Comparison of number of males that dispersed less than the median dispersal distance of females to number of females that dispersed less than the median dispersal distance of males, Comox Burn, 1969–1979.

G test: $G = 26.58$, df = 1, $n = 199$, $p < 0.001$.

[9] Comparison of distances from where birds were marked as juveniles and settled as yearlings or adults between broodmates in sibling pairs of males, females, and those of mixed sex, Comox Burn, 1969–1979.

ANOVA: $F_{2,32} = 0.67$, $p > 0.53$, n.s.

[10] Number of male:male siblings that settled <1 km apart compared to number of siblings in female:female plus mixed sex pairs that did so, Comox Burn.

G test: $G = 4.57$, df = 1, $n = 22$, $p < 0.04$.

[11] Comparison of distances between yearling to adult spring home ranges and distances between adult to adult spring home ranges, data for Comox Burn and Hardwicke Island combined.

Mann–Whitney U test: $U = 1810$, $n_1 = 57$, $n_2 = 79$, $0.06 > p > 0.05$, n.s.

[12] Comparison of distances between nest sites of banded females: yearling to adult sites vs. adult to adult sites vs. nest sites within years (renests).

ANOVA: $F_{2,38} = 1.00$, $p > 0.38$, n.s.

[13] Comparison of sizes of home ranges of yearling males at Comox Burn from mid April to mid May to those from mid May to mid June, 1976–1977.

Mann–Whitney U test: $U = 86.5$, $n_1 = 17$, $n_2 = 22$, $p < 0.01$.

[14] Regression of size of territories: (a) at Middle Quinsam, Comox Burn, and Hardwicke Island and (b) those localities plus Eiby Creek–Green Mt., Skalkaho, and Sheep River, on density of territorial males at the respective areas.

(a) $y = 2.184 - 0.016x$; $F_{1,2} = 17.56$, $R = 0.95$, $p < 0.05$.

(b) $y = 1.501 - 0.008x$; $F_{1,5} = 0.86$, $R = 0.38$, $p > 0.60$, n.s.

[15] Comparison of the dispersion of male territories at Skalkaho (1986) to a random distribution (Clark and Evans 1954) for (a) the entire study area and (b) forested plant communities only.

(a) Nearest Neighbor Test: $R = 1.09$, $c = 1.52$, $n = 72$, $p > 0.05$, n.s.

(b) Nearest Neighbor Test: $R = 1.18$, $c = 2.83$, $n = 71$, $p < 0.01$.

[16] Comparison of distances of feeding sites from nest of one yearling female to those of another at Comox Burn.

Mann–Whitney U test: $U = 3.0$, $n_1 = 3$, $n_2 = 10$, $p < 0.04$.

Chapter 18. Population Parameters

[1] Comparison of sex ratios of wing-tagged chicks to a ratio of 1:1 at (a) Comox Burn, (b) Hardwicke Island; (c) of that at Comox Burn to that at Hardwicke Island, and (d) of that at Comox Burn and Hardwicke Island combined to a ratio of 1:1.

(a) G test: $G = 5.12$, df = 1, $n = 165$, $p < 0.03$.

(b, c) G tests: $G = 1.09$ and 1.70, both df = 1, $n = 368$ and 533, $p = 0.29$ and 0.19, both n.s.

(d) G test: $G = 4.51$, df = 1, $n = 533$, $p < 0.04$.

[2] Comparison of sex ratios of leg-banded chicks to a ratio of 1:1 at (a) Comox Burn, (b) Hardwicke Island, and (c) Comox Burn and Hardwicke Island combined.

(a–c) G tests: all G values between 0.005 and 0.39, all df = 1, n values between 313 and 1205, p values between 0.53 and 0.94, all n.s.

[3] Comparison of the sex ratio of leg-banded chicks to a ratio of 1:1 on the Methow Game Range.

G test: $G = 0.15$, df = 1, $n = 523$, $p = 0.69$, n.s.

[4] Comparison of sex ratios of juveniles killed by hunters to a ratio of 1:1 at (a) Campbell River, (b) Copper Canyon, (c) Ash River, (d) Courtenay, and (e) Cumberland.

(a) G test: $G = 12.50$, df = 1, $n = 372$, $p < 0.001$.

(b-e) G tests: G values between 0.05 and 0.89, all df = 1, n values between 55 and 1051, p values between 0.34 and 0.82, all n.s.

[5] Comparison of sex ratios of juveniles killed by hunters to a ratio of 1:1 at (a) Conconully, (b) Chumstick, (c) Eight Mile Creek, (d) Middle Park, 1975–1985, and (e) Middle Park, 1978 excluded.

(a) G test: $G = 17.71$, df = 1, $n = 1752$, $p < 0.001$.

(b) G test: $G = 3.07$, df = 1, $n = 750$, $0.10 > p > 0.05$, n.s.

(c) G test: $G = 0.19$, df = 1, $n = 84$, $p > 0.66$, n.s.

(d) G test: $G = 4.61$, df = 1, $n = 2532$, $p < 0.04$.

(e) G test: $G = 0.48$, df = 1, $n = 1880$, $p > 0.48$, n.s.

[6] Comparison of sex ratios of juveniles among museum specimens to a ratio of 1:1 for (a) coastal races, (b) interior races, and (c) coastal and interior races combined.

(a, b) G tests: $G = 2.96$ and 2.76, both df = 1, $n = 164$ and 265, both p values $0.10 > p > 0.05$, both n.s.

(c) G test: $G = 5.61$, df = 1, $n = 429$, $p < 0.02$.

[7] Comparison of sex ratios of yearlings to a ratio of 1:1 at (a) Comox Burn, (b) Hardwicke Island, (c) Ash River, and (d) Comox Burn, Hardwicke Island, and Ash River combined.

(a–c) G tests: G values between 0.65 and 2.31, all df = 1, n values between 206 and 306, p values between 0.12 and 0.42, all n.s.

(d) G test: $G = 2.85$, df = 1, $n = 775$, $0.10 > p > 0.05$, n.s.

[8] Comparison of sex ratios of yearlings removed during experiments to a ratio of 1:1 at (a) Middle Quinsam and (b) Tsolum Main.

(a, b) G tests: $G = 2.34$ and 0.06, both df = 1, $n = 35$ and 64, $p = 0.12$ and 0.80, both n.s.

[9] Comparison of sex ratios of yearlings to a ratio of 1:1 at (a) Sheep River (1955–1962) and (b) Sheep River (1955–1959, 1962).

(a) G test: $G = 15.54$, df = 1, $n = 86$, $p < 0.001$.

(b) G test: $G = 2.60$, df = 1, $n = 47$, $p > 0.10$, n.s.

[10] Comparison of sex ratios of yearlings killed by hunters to a ratio of 1:1 at (a) Campbell River, (b) Courtenay, (c) Copper Canyon, (d) Chumstick, (e) Conconully, and (f) Middle Park.

(a–c) G tests: G values between 28.82 and 134.11, all df $= 1$, n values between 50 and 158, all p values <0.001.

(d) G test: $G = 2.50$, df $= 1$, $n = 58$, $p > 0.11$, n.s.

(e, f) G tests: $G = 32.93$ and 10.17, both df $= 1$, $n = 146$ and 417, $p < 0.001$ and < 0.01.

[11] Comparison of sex ratios of adults removed during experiments to a ratio of 1:1 at (a) Middle Quinsam and (b) Tsolum Main.

(a, b) G tests: $G = 2.01$ and 0.01, both df $= 1$, $n = 72$ and 125, $p > 0.15$ and > 0.92, both n.s.

[12] Comparison of sex ratios of adults to a ratio of 1:1 at (a) Comox Burn and (b) Hardwicke Island.

(a, b) G tests: $G = 5.38$ and 25.00, both df $= 1$, $n = 1440$ and 1373, $p < 0.03$ and < 0.001.

[13] Comparison of the sex ratio of adults at Ash River to a ratio of 1:1.

G test: $G = 3.30$, df $= 1$, $n = 851$, $0.10 > p > 0.06$, n.s.

[14] Comparison of sex ratios of adults killed by hunters to a ratio of 1:1 at (a) Campbell River, (b) Copper Canyon, (c) Ash River, (d) Eight Mile Creek, and (e) Middle Park.

(a–c) G tests: G values between 63.77 and 173.15, all df $= 1$, n values between 46 and 1146, all p values <0.001.

(d, e) G tests: $G = 0.51$ and 0.46, both df $= 1$, $n = 49$ and 1698, $p = 0.47$ and 0.49, both n.s.

[15] Comparison of sex ratios of adults and yearlings combined to a ratio of 1:1 at (a) Lower Quinsam, (b) Ash River, (c) Comox Burn, and (d) Green Mountain.

(a–d) G tests: G values between 0.00 and 1.13, all df $= 1$, n values between 104 and 2186, all p values between 0.28 and 1.00, all n.s.

[16] Comparison of the ratio of yearling to adult males among years at (a) Comox Burn, 1969–1978; and (b) Hardwicke Island, 1979–1984.

(a, b) G tests: $G = 36.99$ and 12.56, df $= 9$ and 5, $n = 815$ and 723, $p < 0.001$ and < 0.03.

[17] Comparison of the ratio of yearling to adult females among years at (a) Comox Burn, 1969–1978; (b) Hardwicke Island, 1979–1984; and (c) for combined data for all years between Comox Burn and Hardwicke Island.

(a–c) G tests: G values between 12.27 and 24.81, df $= 9$, 5, and 1, n values between 760 and 1900, all p values between <0.01 and <0.001.

[18] Comparison of the ratio of yearling to adult females between (a) those removed at Middle Quinsam in 1970 to those removed at Comox Burn in 1970, (b) those on the removal plot to those on the control plot at Middle Quinsam, and (c) those on the removal plot to those on the control plot at Comox Burn.

(a–c) G tests: G values between 0.04 and 0.31, all df $= 1$, n values between 88 and 168, all p values between 0.58 and 0.83, all n.s.

[19] Comparison of the ratio of yearling to adult females among years at (a) Middle Quinsam, 1959–1962; (b) Ash River, 1968–1971; (c) Sheep river, 1955–1962; (d) Methow Game Range, 1957–1961; and (e) Skalkaho, 1962–1967.

(a) G test: $G = 4.13$, df $= 3$, $n = 283$, $p = 0.25$, n.s.

(b) G test: $G = 12.89$, df $= 3$, $n = 664$, $p < 0.01$.

(c, d) G tests: $G = 9.69$ and 3.40, df $= 7$ and 4, $n = 210$ and 132, $p > 0.20$ and 0.49, both n.s.

(e) G test: $G = 12.84$, df $= 5$, $n = 191$, $p < 0.03$.

[20] Comparison of the ratio of yearling to adult females between combined coastal subspecies and combined interior subspecies among museum specimens.

G test: $G = 0.04$, df $= 1$, $n = 487$, $p > 0.85$, n.s.

[21] Comparison of the annual ratios of juveniles to yearlings plus adults among hunter-killed birds at (a) Campbell River, 1962–1964; (b) Courtenay, 1970–1979; (c) Chumstick, 1953–1964; (d) Conconully, 1953–1964; (e) Eight Mile Creek, 1959–1961; (f) Middle Park, 1975–1982; (g) Idaho, 1952–1954; and (h) Montana, 1957–1966.

(a) G test: $G = 0.04$, df $= 2$, $n = 755$, $p > 0.98$, n.s.

(b–h) G tests: G values between 9.95 and 124.93, df between 2 and 11, n values between 149 and 9721, all p values between <0.04 and <0.001.

[22] Comparison of the ratio of juveniles to yearlings plus adults among hunter-killed birds between all coastal subspecies, samples combined, and all interior subspecies, samples combined.

G test: $G = 116.00$, df $= 1$, $n = 24{,}773$, $p < 0.001$.

[23] Regression of percent juveniles in hunter-kill at Courtenay on juveniles produced per female at Comox Burn, 1970–1977 (except 1974).

$y = 42.766 + 3.521x$; $F_{1,5} = 0.29$, $R = 0.24$, $p > 0.61$, n.s.

[24] Comparison of the ratio of juveniles to yearlings plus adults between combined coastal subspecies and combined interior subspecies among museum specimens.

G test: $G = 2.55$, df $= 1$, $n = 695$, $p > 0.11$, n.s.

[25] Comparison of age-specific survival among (a) males 1–12 years of age and (b) males 2–12 years of age, Comox Burn, 1962–1977 (ages 7–12 combined because of small samples).

(a) G test: $G = 17.31$, df $= 6$, $n = 622$, $p < 0.01$.

(b) G test: $G = 10.70$, df $= 5$, $n = 427$, $0.10 > p > 0.05$, n.s.

[26] Comparison of age-specific survival of 1–8 year-old females at Comox Burn, 1969–1977 (ages 6–8 combined because of small samples).

G test: $G = 4.75$, df $= 5$, $n = 790$, $p > 0.44$, n.s.

[27] Comparison of age-specific survival among (a) males 1–5 years of age and (b) males 2–5 years of age, Hardwicke Island, 1979–1984 (ages 4–5 combined because of small samples).

(a) G test: $G = 21.51$, df $= 3$, $n = 329$, $p < 0.001$.

(b) G test: $G = 5.47$, df $= 2$, $n = 158$, $0.10 > p > 0.05$, n.s.

[28] Comparison of age-specific survival of 1–5 year-old females at Hardwicke Island, 1979–1984 (ages 4–5 combined because of small samples).

G test: $G = 4.25$, df $= 3$, $n = 707$, $p > 0.23$, n.s.

[29] Comparison of average annual survival at Ash River of (a) yearling to adult males, (b) yearling to adult females, and (c) adult males to yearling and adult females (combined), 1968–1971.

(a) G test: $G = 4.29$, df $= 1$, $n = 215$, $p < 0.04$.

(b) G test: $G = 3.91$, df $= 1$, $n = 401$, $p > 0.95$, n.s.

(c) G test: $G = 29.02$, df $= 1$, $n = 558$, $p < 0.001$.

[30] Comparison of annual survival of banded (a) yearling males, (b) adult males, and (c) adult females, among the years 1969–1977, Comox Burn$_{cp}$.

(a) G test: $G = 10.23$, df $= 7$, $n = 151$, $p > 0.17$.

(b) G test: $G = 5.80$, df $= 7$, $n = 596$, $p > 0.56$.

(c) G test: $G = 8.45$, df $= 7$, $n = 540$, $p > 0.29$.

[31] Comparison of survival of banded yearling females at Comox Burn$_{cp}$ among the years: (a) 1969–1977 and (b) 1969–1976.

(a) G test: $G = 14.09$, df $= 7$, $n = 282$, $p < 0.05$.

(b) G test: $G = 9.09$, df $= 6$, $n = 265$, $p > 0.12$, n.s.

[32] Comparison of mean annual survival of banded grouse at Comox Burn$_{cp}$, 1969–1977, between (a) yearling and adult males, (b) yearling and adult females, (c) yearling males and yearling plus adult females, and (d) adult males and yearling plus adult females.

(a) G test: $G = 6.70$, df = 1, $n = 747$, $p < 0.01$.

(b) G test: $G = 1.99$, df = 1, $n = 822$, $p > 0.15$, n.s.

(c, d) G tests: $G = 4.41$ and 60.24, both df = 1, $n = 973$ and 1418, $p < 0.04$ and < 0.001.

[33] Comparison of annual survival of (a) yearling males and (b) adult males, among the years 1979–1984 at Hardwicke Island.

(a) G test: $G = 6.92$, df = 4, $n = 176$, $p > 0.14$, n.s.

(b) G test: $G = 8.55$, df = 4, $n = 545$, $0.10 > p > 0.05$, n.s.

[34] Comparison of annual survival of banded females at Hardwicke Island of (a) yearling females, 1979–1984, (b) adult females, 1979–1984, and (c) yearling females, for the combined years 1979–1981 versus 1982–1984.

(a–c) G tests: G values between 12.85 and 15.78, df = 4, 4, and 1, $n = 349$ and 780, all p values between <0.02 and <0.001.

[35] Comparison of mean annual survival of banded grouse at Hardwicke Island, 1979–1984, between (a) yearling and adult males, (b) yearling males and all females, and (c) adult males and all females.

(a) G test: $G = 9.68$, df = 1, $n = 721$, $p < 0.01$.

(b) G test: $G = 2.22$, df = 1, $n = 1305$, $p > 0.13$, n.s.

(c) G test: $G = 8.10$, df = 1, $n = 1674$, $p < 0.01$.

[36] Comparison of mean annual survival of banded grouse at Comox Burn, 1969–1977, to that at Hardwicke Island, 1979–1984, for (a) yearling males, (b) adult males, (c) yearling females, and (d) adult females.

(a–c) G tests: G values between 5.21 and 14.21, all df = 1, n values between 327 and 1141, p values between <0.03 and <0.001.

(d) G test: $G = 0.09$, df = 1, $n = 1320$, $p > 0.76$, n.s.

[37] Comparison of mean annual survival of banded adult males in the West Fork of the Bitterroot Valley to that at Skalkaho, 1963–1967.

G test: $G = 0.44$, df = 1, $n = 180$, $p > 0.50$, n.s.

[38] Comparison of mean annual survival of banded yearling males at Sheep River to that at (a) Middle Quinsam, (b) Comox Burn, (c) Hardwicke Island, and (d) Ash River.

(a, b) G tests: $G = 11.62$ and 10.22, both df = 1, $n = 65$ and 279, $p < 0.001$ and < 0.01.

(c, d) G tests: $G = 3.34$ and 3.50, both df = 1, $n = 191$ and 94, both p values $0.10 > p > 0.05$, n.s.

[39] Comparison of mean annual survival of banded adult males at Sheep River to that at (a) Skalkaho–Bitterroot Valley, (b) Lower Quinsam, (c) Middle Quinsam, (d) Comox Burn, (e) Hardwicke Island, and (f) Ash River.

(a–f) G test: G values between 4.00 and 17.94, all df = 1, n values between 175 and 961, p values between <0.05 and <0.001.

[40] Regression of percent return to Hardwicke Island study areas of wing-tagged and leg-banded juveniles on age at time of marking, 1979–1984.

$y = 7.022 + 2.278x$; $F_{1,9} = 24.31$, $R = 0.85$, $p < 0.01$.

[41] Comparison of percent return of banded chicks between Comox Burn and Hardwicke Island for (a) those marked at 9–10 weeks of age at both areas and (b) those marked at 9–10 weeks of age at Comox Burn and at ≥ 11 weeks of age at Hardwicke Island.

(a) G test: $G = 6.06$, df = 1, $n = 255$, $p < 0.02$.

(b) G test: $G = 0.20$, df = 1, $n = 185$, $p > 0.65$, n.s.

[42] Comparison of percent of known-aged females with and without brood among all age classes at (a) Comox Burn, 1969–1978, and (b) Hardwicke Island, 1979–1984; and among adult only age classes at (c) Comox Burn, and (d) Hardwicke Island (age classes 5–8 combined at Comox Burn).

(a, b) G tests: $G = 51.07$ and 15.65, df = 4 and 5, $n = 529$ and 623, $p < 0.001$ and < 0.01.

(c, d) G tests: $G = 1.80$ and 2.79, df = 3 and 4, $n = 231$ and 300, $p > 0.61$ and 0.59, both n.s.

[43] Comparison of percent of known-age females with and without brood between Comox Burn and Hardwicke Island for (a) yearlings and (b) adults.

(a) G test: $G = 26.82$, df = 1, $n = 612$, $p < 0.001$.

(b) G test: $G = 1.23$, df = 1, $n = 531$, $p > 0.26$, n.s.

[44] Comparison of percent of banded females with and without brood among years, 1969–1977, at Comox Burn for (a) yearlings, (b) adults, and (c) both age classes combined; and at Hardwicke Island, 1979–1984, for (d) yearlings, (e) adults, and (f) both age classes combined.

(a) G test: $G = 18.06$, df = 8, $n = 289$, $p < 0.03$.

(b) G test: $G = 12.01$, df = 8, $n = 462$, $p > 0.15$, n.s.

(c) G test: $G = 21.02$, df = 8, $n = 751$, $p < 0.01$.

(d) G test: $G = 6.83$, df = 5, $n = 323$, $p > 0.23$, n.s.

(e) G test: $G = 21.66$, df = 5, $n = 727$, $p < 0.001$.

(f) G test: $G = 10.93$, df = 5, $n = 1050$, $0.10 > p > 0.50$, n.s.

[45] Comparison of percent of all banded females with and without brood at Comox Burn to that at Hardwicke Island for (a) adults and (b) yearlings and adults combined.

(a, b) G tests: $G = 4.60$ and 34.72, both df = 1, $n = 1189$ and 1801, $p < 0.04$ and < 0.001.

[46] Comparison of percent of females sighted with and without brood in June to that in July–August at two areas of the Methow Valley.

G test: $G = 25.60$, df = 1, $n = 283$, $p < 0.001$.

[47] Comparison of percent of banded yearling females with and without brood at Ash River to that at (a) Comox Burn and (b) Hardwicke Island; and of percent of banded adult females at Ash River to that at (c) Comox Burn and (d) Hardwicke Island.

(a) G test: $G = 17.39$, df = 1, $n = 612$, $p < 0.001$.

(b, c) G tests: $G = 1.09$ and 2.44, both df = 1, $n = 646$ and 797, $p > 0.29$ and 0.87, both n.s.

(d) G test: $G = 3.12$, df = 1, $n = 1062$, $0.10 > p > 0.05$, n.s.

[48] Comparison of mean annual late-summer brood sizes of yearling females to those of adult females at (a) Comox Burn and (b) Hardwicke Island.

(a, b) Student's t tests: $t = -0.69$ and -1.12, df = 16 and 10, $p = 0.51$ and 0.29, both n.s.

[49] Comparison of mean annual late-summer brood sizes of all females among years at (a) Comox Burn, 1969–1977, and (b) Hardwicke Island, 1979–1984.

(a) ANOVA: $F_{8,842} = 5.76$, $p < 0.001$.

(b) ANOVA: $F_{5,1135} = 20.39$, $p < 0.001$.

[50] Comparison of mean annual late-summer brood sizes at Comox Burn, 1969–1977, to those at Hardwicke Island, 1979–1984, for (a) yearling females, (b) adult females, and (c) all females.

(a–c) Student's t tests: t values between 3.36 and 3.60, all df = 13, all p values <0.01.

[51] Relationship between percent of all females with brood and mean brood size at (a) Comox Burn among the years 1969–1977 and (b) Hardwicke Island among the years 1979–1984.

(a) $y = 0.775 + 0.034x$; $F_{1,7} = 2.86$, $R = 0.54$, $p > 0.13$, n.s.
(b) $y = 9.36 + 0.141x$; $F_{1,4} = 34.54$, $R = 0.94$, $p < 0.01$.

[52] Comparison of percent of banded females with and without brood in 1969, 1970, and 1971 yearling cohorts at Comox Burn to that of adults in the same years.
G test: $G = 7.87$, df $= 1$, $n = 198$, $p < 0.01$.

Chapter 19. Predators

[1] Comparison of temporal pattern of predation on adult plus yearling males to that on adult plus yearling females by 1/2-month periods, data for recent kills at Comox Burn and Hardwicke Island combined.
G test: $G = 20.84$, df $= 8$, $n = 172$, $p < 0.01$.

[2] Comparison of the ratio of yearling to adult males killed by predators to an expected ratio of 30:70, data for Comox Burn and Hardwicke islands combined; includes recent and old kills.
G test: $G = 1.53$, df $= 1$, $n = 115$, $p > 0.21$, n.s.

[3] Comparison of the ratio of yearling to adult females killed by predators to an expected ratio of (a) 30:70 and (b) 40:60, data for Comox Burn and Hardwicke Island combined; includes recent and old kills.
(a) *G* test: $G = 6.99$, df $= 1$, $n = 77$, $p < 0.01$.
(b) *G* test: $G = 0.48$, df $= 1$, $n = 77$, $p > 0.48$, n.s.

[4] Comparison of the ratio of (a) yearling males to yearling females killed by predators and (b) adult males to adult females killed by predators, both to a ratio of 1:1; data for Comox Burn and Hardwicke Island combined and includes recent and old kills.
(a) *G* test: $G = 1.49$, df $= 1$ $n = 63$, $p > 0.48$, n.s.
(b) *G* test: $G = 15.19$, df $= 1$, $n = 130$, $p < 0.001$.

[5] Comparison of the number of adult plus yearling males and adult plus yearling females killed by raptors or by mammals at Comox Burn to that at Hardwicke Island.
G test: $G = 0.93$, df $= 1$, $n = 55$, $p > 0.33$, n.s.

[6] Comparison of the number of adult plus yearling males killed by raptors or by mammals to that of adult plus yearling females, data for Comox and Hardwicke islands combined.
G test: $G = 0.47$, df $= 1$, $n = 155$, $p > 0.49$, n.s.

[7] Comparison of the number of adult and yearling males plus adult and yearling females killed by raptors or by mammals to that of juveniles; data for Comox Burn and Hardwicke Island combined.
G test: $G = 12.64$, df $= 1$, $n = 175$, $p < 0.001$.

[8] Comparison of the number of adult and yearling males to the number of adult and yearling females struck by predators and known to be killed or that may have escaped; data for Comox Burn and Hardwicke Island combined.
G test: $G = 3.68$, df $= 1$, $n = 217$, $0.10 > p > 0.05$.

[9] Comparison of the success of witnessed attacks on grouse between those induced by the observer and those not so induced.
G test: $G = 6.28$, df $= 1$, $n = 49$, $p < 0.01$.

[10] Comparison of the number of adult and yearling males plus adult and yearling females killed by raptors or by mammals to that of juveniles, data from interior populations.
G test: $G = 5.14$, df $= 1$, $n = 34$, $p < 0.03$.

[11] Comparison of the amount of predation by raptors or by mammals between juveniles on autumn or winter range.
G test: $G = 8.95$, df $= 1$, $n = 201$, $p < 0.01$.

[12] Comparison of nest losses during laying to those during incubation at (a) Comox Burn and (b) Hardwicke Island.
(a, b) *G* tests: $G = 1.38$ and 0.81, both df $= 1$, $n = 1470$ and 1352, $p > 0.23$ and > 0.36, both n.s.

[13] Comparison of nest losses between Comox Burn and Hardwicke Island during (a) laying and (b) incubation.
(a) *G* test: $G = 0.76$, df $= 1$, $n = 143$, $p > 0.38$, n.s.
(b) *G* test: $G = 13.21$, df $= 1$, $n = 2679$, $p < 0.001$.

[14] Comparison of number of nests with poor, moderate, or good cover between yearling and adult hens, data from Comox Burn.
G test: $G = 1.26$, df $= 2$, $n = 88$, $0.10 > p > 0.05$, n.s.

[15] Comparison of the number of successful nests among the cover categories poor, moderate, and good, data from Comox Burn.
G test: $G = 2.61$, df $= 2$, $n = 149$, $p > 0.26$, n.s.

Chapter 20. Disease, Parasites, and Physical Anomalies

[1] Comparison of prevalences of (a) *L. bonasae*, (b) *T. avium*, (c) *H. mansoni*, and (d) microfilariae between adult plus yearling males and adult plus yearling females.
(a, b) *G* tests: $G = 1.09$ and 0.04, both df $= 1$, both $n = 1025$, $p > 0.29$ and > 0.84, both n.s.
(c) *G* test: $G = 3.68$, df $= 1$, $n = 1025$, $0.06 > p > 0.05$, n.s.
(d) *G* test: $G = 7.76$, df $= 1$, $n = 1025$, $p = 0.01$.

Appendix 2. Annotated List of Physical Anomalies

Integumentary

Superficial wounds and sores:

5877 (band no.), ad fem, 27 June 1972—two wounds on brood patch, one ~13 mm in diam., right eye injured a bit, 5–6 rectrices missing, left middle claw missing; mass = 815 g, normal. Ash River.

6546, ad fem, 7 June 1973—small scab right side of brood patch; mass = 860 g, normal. Comox Burn.

10345, ylg fem, 25 June 1974—4 × 5 cm hard scab centre of brood patch; nest hen inside deer fence, has flown into fence; some eggs in nest broken, perhaps by scab?; one hatched 25 June; fem in fair flesh; mass = 750 g, marginally normal. Comox Burn.

Necropsy 70-93, ylg fem, 3 July 1979—infection under skin of brood patch; dark greenish brown matter forms swelling ~2 cm diam.; mass = 770 g, normal. Comox Burn.

2661, ylg fem, 5 June 1969—wound on right shoulder; can fly; no mass recorded. Comox Burn.

4207, juv male, 51 days of age,13 August 1970—tip of middle toe, right foot, swollen and infected; mass = 440 g, normal. Comox Burn.

5453, ad fem, 5 August 1971—shotgun pellet under skin of right elbow; mass = 900 g, normal. Comox Burn.

10289, ad male, 10 May 1974—scar on right foot, partly healed; mass = 1330 g, normal. Comox Burn.

10831, ylg fem, 3 July 1975—small bare spot, ~1.5 cm diam., left side of crown, slightly swollen; mass = 720 g, subnormal. Comox Burn.

11386, ylg fem, 12 August 1976—slight swelling, conjunctiva of left eye; mass = 840 g, normal. Comox Burn.

12761, juv sex?, 48 days of age, 25 July 1979—1 × 1.5 cm sore top of right foot; 2 × 2.2 cm sore bottom of left foot; mass = 340 g, normal. Hardwicke Island.

12477, juv sex?, 47 days of age, 30 July 1979—cut on toe, left foot, beginning to scar over; mass = 301 g, normal. Hardwicke Island.

13363, juv fem, 6 October 1980—bad gash on neck, infected and greenish; mass = 850 g, normal. Hardwicke Island.

13152, ad male, 15 May 1981—scars both sides of head just behind eyes; mass = 1270 g, normal. Hardwicke Island.

12499, ad male, 22 August 1982—right eye missing, large scab-like growth over eye socket; growth appears old; bird appears healthy; mass = 1140 g, subnormal. Hardwicke Island.

13757, ad male, 6 March 1982—swelling beneath left eye; eye watery; mass = 1360 g, normal. Hardwicke Island.

14066, ylg male, 21 April 1983—1 × 1.5 cm scab right side of breast; skin yellowish around scab, new pinfeathers coming in; mass = 1130 g, normal. Hardwicke Island.

20763, juv sex?, 44 days of age, 30 June 1968—scabbed over sore at heel of right foot, swollen; mass = 184 g, subnormal. Methow Valley.

20750, juv sex?, 46 days of age, 2 July 1968—extensive wound on right tibiotarsus, skin torn but healing; bird walks and runs normally; mass = 335 g, normal. Methow Valley.

14149, ad male, 23 April 1984—4 × 22 mm scar anterior end of 22 × 40 mm bare patch, centre of lower back; mass = 1227 g, normal. Methow Valley.

14372, ad fem, 17 July 1986—3 × 5 cm bare area on back with scar in middle, missing seven rectrices; mass = 840 g, normal. Hudson Bay Mt

Deeper wounds

2673, ad male, 19 June 1970—piece of wood 7 mm × 5 cm forced through skin from front between left thigh and body, anterior end outside body and skin healed around and to it; a second piece, 3 mm × 3.5 cm, projecting dorsally from body posterior to thigh, likely an extension of the first that had broken off; mass = 1330 g, normal. Comox Burn.

7656, juv male, 23 August 1958—old wound on stomach, part of intestine exposed; wound dried and healing, part of tail missing; mass = 799 g, normal. Methow Valley.

No band or wing tag, juv sex?, 5 days of age, 12 June 1978—prickly pear cactus spine through one foot; mass = 32 g, normal. Bothwick, NV.

Tumour and wart-like growths

1327, ad fem, 26 May 1964—large bulbous tumours on various parts of body; no mass recorded. Comox Burn.

5680, ylg fem, 13 May 1972—several large wart-like knots in region of proximal phalanges, left foot; mass = 700 g, subnormal. Comox Burn.

10472, juv sex?, 61 days of age, 16 August 1974—calloused growth on most proximal phalanges of inner toe, right foot; mass = 540 g, normal. Comox Burn.

11879, ad fem, 6 May 1979—2 cm diam. growth (or scab?), bottom of left metatarsus, halfway between toes and heel; bird in good condition; mass = 990 g, normal. Hardwicke Island.

12908, juv fem, 50 days of age, 8 August 1979—2 cm diam. growth on outer toe, left foot; start of a growth on mid toe, proximal phalange; mass = 320 g, normal. Hardwicke Island.

12977, juv fem, 82 days of age, 28 August 1979—2.5 cm diam. orangish growth near tip of manus of left wing; mass = 560 g, normal. Hardwicke Island.

12093, ylg fem, 2 May 1980—left side of head, large growth on left maxilla, extends from beak to within 3 mm of eye and into mouth onto left palate; yellowish and scabby. Also, 1.5 cm wide growth bottom of left metatarsus; extends from heel to base of toes, but constricted by bands; mass = 870 g, normal. Hardwicke Island.

13767, juv sex?, 43 days of age, 28 July 1981—yellowish growths on back of head near right ear and on rump near uropygium; skin bare; mass = 264 g, normal. Hardwicke Island.

13742, juv fem, 75 days of age, 24 August 1981—large molelike growth on neck; mass = 535 g, normal. Hardwicke Island.

13913, juv male, 64 days of age, 26 August 1981—dark brown molelike growths on neck; mass = 565 g, normal. Hardwicke Island.

14020, ad male, 20 August 1982—2–3 mm diam. wart, leading edge of right eyelid; mass = 1230 g, normal. Hardwicke Island.

7393, juv fem, 6 August 1959—wart-like growth on left eye (eyelid?); mass = 493 g, normal. Methow Valley.

Scalelike growths

4136, ylg male, 8 August 1969—bare and hardened yellowish skin, ~6 mm above and below joint of heel, right leg; no apparent impediment; mass = 1200 g, normal. Comox Burn.

6324, juv sex?, 25 days of age, 24 July 1972—right foot scaly and toes crooked; mass = 97 g, subnormal (broodmate = 158 g). Comox Burn.

10377, ad male, 27 June 1974—skin on bottoms of both feet dry, loose, and scaly, peeling off; new skin underneath appears normal; mass = 1290 g, normal. Comox Burn.

20739, juv sex?, 34 days of age, 27 June 1968—feet and hocks gnarled and scaly, outer toes twisted outwards; mass = 238 g, normal. Methow Valley.

14225, ad male, 21 May 1984—scaly growth on outer toe, left foot; mass = 1170 g, normal. Methow Valley.

Skeletal

Perhaps inherent

3837, ad male, 11 May 1970, toe missing; mass = 1240 g, normal. Comox Burn.

10616, ylg fem, 22 May 1975—claw and part of outside toe, left foot, missing; mass = 940 g, normal. Comox Burn.

Wing tag 4011, juv sex?, 11 days of age, 6 July 1975—mandibles offset to the right from maxillae so that tips of upper and lower parts of beak were ~2–3 mm apart; chick appeared healthy and active; mass = 42 g, normal. Comox Burn.

11134, ylg fem, 28 July 1975—outer toe missing, mid toe bent downward at joint between first and second phalanges, claw long and unworn, right foot; mass = 740 g, marginally subnormal. Comox Burn.

12241, ad male, 27 May 1979—no claw, inside toe, left foot; mass = 1225 g, normal. Hardwicke Island.

12699, ad fem, 24 July 1979—manus of left wing missing and bird cannot fly; no chicks seen but behaviour suggests she may have had brood; brood patch present; mass = 900 g, normal. Hardwicke Island.

12088, juv male, 48 days of age, 8 August 1979—mid toe left foot curved abnormally; mass = 360 g, normal. Hardwicke Island.

Necropsy 81-18, juv fem, 7 days of age, June 1981—only smallest toe of right foot has a claw, only inner toe of left foot has a claw; mass = 29 g, subnormal. Hardwicke Island.

14020, ad male, 20 August 1982—no claw, mid toe right foot; mass = 1230 g, normal. Hardwicke Island.

No band or wing tag, juv sex?, 1 day of age, 2 June 1983—toes curled, bird appeared unhealthy, mass = 21 g, subnormal. Hardwicke Island.

14160, ad male, 29 May 1983—no claw outside toe right foot; no mass recorded. Hardwicke Island.

14170, ylg fem, 7 July 1983—no outside toe right foot; mass = 790 g, normal. Hardwicke Island.

15116, ad fem, 3 August 1957—toes small and abnormal, phalanges appear shortened; mass = 738 g, subnormal. Methow Valley.

Perhaps a result of injury

No band or wing tag, juv sex?, ~7 days of age, 6 July 1963—left eye mattering and partially closed; no mass recorded. Comox Burn.

1589, juv sex?, 43 days of age, 12 August 1964—large lump ~12 mm diam. near distal end of radius, appears to have been broken but now healed; chick flies well; mass = 390 g, normal. Comox Burn.

Necropsy 70-53, ad male, 10 June 1970—tibiotarsus once broken, now healed; mass = 1462 g, normal. Comox Burn.

5609, ylg male, 30 April 1972—distal end mid toe and claw, right foot, damaged and swollen, outer toe bent abnormally; mass = 900 g, subnormal. Comox Burn.

10020, juv sex?, 38 days of age, 23 July 1973—right eye red and no visible pupil, appears blind; mass = 192 g, normal. Comox Burn.

10313, ylg fem, 20 May 1974—left metatarsus broken in centre, now healed; large and crooked; following capture, oviduct 1–2 cm out of cloaca, fecal matting in cloacal region; oviduct pushed back in and she flies off strongly; mass = 880 g, normal. Comox Burn.

4148, ad male—banded as juv 1969; resighted each year on territory 1971–1977; hooting on territory 31 May 1977 (very lame on left foot); hooting on territory 23 June 1977 and recaptured, lower leg gone at distal end of the femur; no further sightings. Loss of lower leg appears to have resulted from infection related to injury (perhaps, improperly applied bands?); no record of lameness prior to 1977; mass, 23 June = 1050 g, subnormal. Comox Burn.

12020, ad male, 30 July 1979—outer toe left foot abnormally enlarged; swollen or malformed?; mass = 1240 g, normal. Hardwicke Island.

12838, juv male, 68 days of age, 23 August 1979—halux on left foot swollen, shorter than on right foot; broken?; mass = 610 g, normal. Hardwicke Island.

14247, ad male, 14 April 1984—left foot gone ~37 mm from proximal end of metatarsus; leg appeared functional; mass = 1156, marginally normal. Methow Valley.

Miscellaneous abormalities

10731, ylg fem, 22 May 1975—red colour band in gizzard; bird not banded prior to collection; mass = 790 g, marginally normal. Comox Burn.

Wing tag 6483, juv sex?, 2 days of age, 22 June 1983—bird "dozey" and likely not able to stand; P2 and P3 stuck together, mass = 26 g, normal. Hardwicke Island.

Adult males are commonly seen with specks of dried blood on the combs, presumably caused by biting flies. Up to 5–10 may be seen on an individual bird. Haemoprotists and haemofilarids may be acquired through these attacks.

Rarely, downy chicks are seen with a carpenter ant (*Campanotus* sp.) clamped by its jaws to the foot or lower leg; usually on day-old chicks in, or just out of, the nest. We suspect such ants were somehow irritated by the chicks and that they soon drop off. No sign of damage has been noted.

Glossary

This glossary is adapted, in part, from various authors and dictionaries and explains terms in the text. The extensive glossary in Van Tyne and Berger (1966) was especially helpful. Other works used include Daubenmire (1968), Fitzgerald (1969), Flexner and Hauck (1987), Hammond (1991), Hjorth (1970), Kenneth (1960), King and Farner (1961), Pekins (1988), Pettingill (1946), Ricklefs (1982), Robbins (1983), Smith (1974), Sturkie (1965), Villee et al. (1979), and Wilson (1975).

adult (also **ad** or **A**). A grouse entering its second year and beyond; beginning 1 January of its second winter. See also **yearling** and **juvenile**.

air sacs. Extensions from the lungs in birds; occurring in the body cavity, under the skin, and in certain bones.

alar tract. Pertaining to feather tracts of the wing.

alternate host. Another species or individual that can harbour a parasite or disease and serve as a source of infection for a species or individual of concern.

alula (also **bastard wing**). Three quill feathers on the first digit of a bird's wing; the feathered "thumb".

annual turnover. See **turnover**.

antebrachium. The forearm.

antisocial. Solitary, living habitually alone, or in pairs. Degree of sociality may vary seasonally and (or) by gender, age, and species. See also **social**.

apteria (pl. of **apterium**). Bare (or downy) areas between the feather tracts (**pterylae**).

arboreal. Tree-frequenting.

ascites. A pathological condition caused by an accumulation of serous fluid in the peritoneal cavity.

association (botanic). A plant community possessing a definite floristic composition.

auricular region. Area around the ear.

auriculars. Feathers growing on the auricular region; may cover the external ear opening.

bastard quill (also **alula**). One of the feathers of the alula.

bioassay. Determination of the biological activity or potency of a substance by testing its effect on an organism.

biome. A biotic community characterized by the distinctive life forms of the principal "climax" species.

BMR (basal metabolic rate). The resting energy metabolism of an animal in the postabsorptive [fasting] state, in a thermoneutral environment. See also **SMR**.

brood. 1. Chicks (or juveniles) belonging to an individual hen (noun). A brood consists of one or more chicks. 2. A hen may keep her chicks warm by brooding them, or chicks may brood under a hen or in an artificial brooder (verb). See also **chick** and **juvenile**.

brood patch. A modified (highly vascular) area of skin on the belly; applied to the surface of the eggs during incubaion.

bursa of Fabricius. A dorsal diverticulum of the proctodeum (most caudal and dorsal part of the cloaca). It atrophies after hatching (rate varies in different groups of birds) and has been used as a criterion of age.

CA–OR–WA. Refers to composite samples of *D.o. sierrae* from California, Oregon, and Washington. These were from various areas in the three states, none of which was a particular study area.

canto (pl. **canti**). A single song, consisting in blue grouse, of 1–7 syllables.

cantus (pl. **cantus**). "A series of notes, generally more than 1 type, uttered in succession so related to form a recognizable sequence . . . in time" ("Thorpe's definition", in Hjorth 1970); of a less rigid construction than a canto.

capital tract. Pertaining to feather tracts of the head.

carpometacarpus. The bone formed by the fusion of carpal and metacarpal bones; the bone to which the primary feathers are attached.

caudal tract. Pertaining to feather tracts of the tail.

cecum (pl. ceca; also **caecum**, pl. caeca). A diverticulum at the junction of the small and large intestines; typically paired when present.

centre of activity. Portion of a home range or territory in which activities may be concentrated.

cervical apteria. Refers to the lateral cervical apteria, 1 on each side of the neck and modified for display in males of some species of grouse, including blue grouse.

chick. A juvenile bird, usually used to refer to those when relatively small; in our use, usually less than half-grown. See also **juvenile**.

clade. A taxonomic group of organisms classified together on the basis of homologous features traced to a common ancestor.

clear-cut. An area from which all trees have been removed by logging.

cloaca. The common chamber which receives the rectum, ureters, and gonaducts (oviduct or sperm ducts); opens to the external orifice, the vent.

clutch (of eggs). The total number of eggs laid for a single nesting.

colon. The large intestine.

community. A naturally occurring assemblage of organisms that live in the same environment. Sometimes separated as plant or animal communities.

Comox Burn$_{\text{cp}}$. This designation with subscript "cp" refers to the control plot at Comox Burn, particularly as compared to the experimental plot, Tsolum Main. Without the subscript, Comox Burn refers to the general area of studies in this region, including Tsolum Main—see 3.1.3.

contour feathers. The outer feathers of the head, neck, body, and limbs.

cornified. Refers to a horny layer of the skin such as, in birds, the beak and nails.

counter-singing. Singing by one bird in response to that of another of the same species; usually birds of the same sex.

cover. Vegetation or non-living elements of the environment (e.g., rocks, caves) that serve as shelter from the weather or concealment from predators.

coverts. The small feathers which overlie the bases of the flight feathers (remiges and rectrices); auricular (pertaining to the ear) feathers are ear coverts.

crepuscular. Active at twilight; dawn or dusk.

crest. A tuft of lengthened feathers on the head; erect, or capable of being erected.

crissum. The under tail coverts.

crop (also **ingluvies**). A ventral diverticulum of the esophagus; used for the temporary storage of food.

crude protein. The total protein in a foodstuff, usually determined by proximate chemical analysis.

crural. Pertaining to the tibia (tibiotarsus). **Crural tract** pertains to feather tracts of the tibia.

culmen. Uppermost ridge, or central longitudinal line, of the upper mandible (the maxilla).

DBH. Diameter of a tree at breast height.

Definitive Basic Plumage. The adult plumage, that following the postjuvenal plumage. In blue grouse, it usually starts to appear at 11–12 months, and is completed at 15–16 months, of age. It is replaced each year.

dendrogram. See **phylogenetic tree**.

dermal. Pertaining to the skin.

dimorphic. Having two forms.

dispersal. Movement of organisms away from the place of birth or from centres of population density to a new area of residence. In our use, a permanent movement, as contrasted to migration. See also **natal dispersal**.

dispersion. Pattern of spacing of individuals.

distal. Farthest from the trunk or midline; referring especially to the segments of the appendages; opposite of proximal.

DNA. Deoxyribonucleic acid, the main component of chromosomes; the material that transfers genetic characteristics in all life forms.

egg-tooth. A horny tubercle near the tip of the upper mandible in the hatching bird. It is shed shortly after hatching; within ~1 day in blue grouse.

endemic. Confined to a certain area or region.

energy cost of detoxification. Energy used to detoxify foods and not available for other metabolic functions.

enteric bacteria. A bacterium that lives in the gastrointestinal system.

epidermis. The outer, nonvascular, nonsensitive layer of the skin.

excreta. Excrement; waste matter, especially the feces and nitrogenous products of metabolism.

feather tracts. See **pteryla**.

fecal. Pertaining to excrement (feces).

fem. Abbreviation for female.

fertility (of eggs). By our definition, the percentage of all eggs that complete the incubation period and hatch, plus those for which there is clear evidence of embryonic development in unhatched eggs.

First Basic Plumage. The postjuvenal plumage; that which replaces the juvenal plumage.

flight feathers. The remiges and rectrices.

FMR (field metabolic rate). The energy cost of free existence.

FMR:BMR ratio. Provides an estimate of the energy cost of free existence relative to that of the BMR.

forb. Broad-leaved flowering plants, as contrasted to grasses and sedges.

galliforms. Birds in the Order Galliformes; grouse, quail, pheasants, etc.

gallinaceous. Pertaining to galliform birds.

gizzard. The ventriculus, the muscular portion of the stomach.

grit. Small stones eaten by some birds, including grouse; they accumulate in the gizzard and aid in the mastication of food.

gular. Pertaining to the throat.

habitat. The natural environment of an organism.

habitat selection. The disproportionate use of available habitats, or portions of habitats.

haemofilarids. Microfilareae (motile embryonic nematodes) living in the blood vascular system of vertebrates.

haemoprotists. Protists (see **Prostista**) living in the blood vascular system of vertebrates.

Hardy–Weinberg Principle. The principle that a population is genetically stable in succeeding generations.

hatchability. By our definition, the percentage of all eggs that complete the incubation period and hatch. Differs from *hatchability of fertile* eggs in that it includes eggs in which there was no evidence of embryonic development. See also **fertitlity**.

hatching success. By our definition, the percentage of eggs that hatched of the total number laid.

heterotroph. An organism that utilizes organic materials as a source of energy and nutrients.

holarctic. Northern regions of the Old and New Worlds.

home range. An area from which intruders may or may not be excluded and within which most normal activities are conducted. Part or all of a home range may be a territory.

hooting. The song of male blue grouse.

humerus. Bone of the upper arm.

ID–OR–WA. Refers to Idaho, Oregon, and Washington, collectively, the region from which Beer (1943) collected food habit samples. These were from various areas in the three states. Interior samples, the vast majority, represent *D.o. pallidus*, referred to as *D.o. richardsonii* by Beer. Coastal samples represent *D.o. fuliginosus*.

integument. Covering, envelope; the skin and its accessory structures, e.g., feathers.

intermediate host. Some parasites require two or more hosts to complete their life cycles. Those for the developmental stages are intermediate hosts.

juvenal. Refers to the plumage immediately succeeding the natal down and preceding the postjuvenal (First Basic) plumage.

juvenile (also **juv** or **J**). A first-year grouse; by our definition, from time of hatch to 31 December of its first winter, following which it is classified as a yearling. See also **chick** and **yearling**.

lek. In its strictest sense, the performance of a group of males that come together for courtship display (Hjorth 1970). Used by some authors to refer to the place where they congregate, which Hjorth defines as an **arena**.

lower critical temperature (also **LCT**). The minimum temperature within the thermoneutral zone and below which metabolism increases for thermoregulation.

manus (hand). The carpometacarpus and its digits; part of the wing that bears the primary feathers.

migration. As used here, seasonal to and fro movements between breeding and wintering areas. See also **dispersal**.

moult. Renewal of plumage; includes the normal loss and replacement of feathers.

natal dispersal. Movement from where an individual is born to where it will breed, or attempt to breed.

Natal Plumage (also **natal down**). Grouse and other galliforms hatch with a dense coat of down. It is replaced by the juvenal plumage in the bird's first summer or early autumn.

nesting success. By our definition, the percentage of nests from which at least one chick hatched.

neutral detergent fiber (NDF). The cell wall residue of plant materials; contains hemicellulose, cellulose, lignin, and cutin.

nidifugous. Said of birds whose young leave the nest shortly after hatching.

nitrogen cost of detoxification. Nitrogen used to detoxify foods and not available for other metabolic functions.

oedema (edema, U.S.). Swelling or thickening of the skin.

oldfield. Land once tilled for agriculture but abandoned for that purpose and reverting to natural plant communities.

old-growth forest. We use this term in a general sense to apply to undisturbed mature forest. Age when old-growth attributes appear will differ with stand composition, e.g., dry lodgepole pine forest (~100 years), as compared to coastal Douglas-fir and western hemlock–Sitka spruce forest (~200–250 years).

opportunity cost. The cost in terms of energy and nutrients by being deterred from feeding on a particular food because of secondary compounds.

ovary. Female sex organ (gonad) which produces the ova (germ cells) of the female.

oviduct. Tubelike passage for the eggs, leading from near the ovary to the cloaca.

pars cervicalus. Section of the esophagus anterior to the crop.

pars thoracica. Section of the esophagus posterior to the crop.

patagial (adj. of patagium). Refers to the patagial membrane, that at the leading edge of the wing, between the distal end of the humerus and proximal end of the radius.

pectinate. Having tooth-like projections, like the teeth of a comb; **pectinations**, as on the sides of the toes of grouse.

phenotype. The group in which an individual is classified on the basis of visible characters.

philopatry. The tendency of animals to remain at certain places, or to return to them.

phylogenetic tree (also **dendrogram**). A graphic depiction of evolutionary relationships in the form of a tree.

pip. To crack or chip a hole through the eggshell, as a young bird beginning to hatch (verb), or the hole that has been pipped (noun).

pistillate cones. Female cones.

plantar digital pads. Pads on the bottom of the toes.

polygynous. Said of males that breed with two or more females.

postjuvenal. Applied to the plumage [and its moult] immediately succeeding the juvenal plumage; in blue grouse, it resembles the adult plumage in most respects.

postovulatory follicle. An ovarian follicle that has shed its ovum.

precocial. Birds that are well developed at hatching; covered with down and able to move about and feed themselves.

primary feather. One of the flight feathers (remiges) attached to the hand (the manus).

promiscuous. Having sexual relations with a number of partners on a casual basis.

Protista. Kingdom of unicellular organisms many of which were formerly included in the Phylum Protozoa.

proventriculus. Glandular portion of the stomach; leads from the esophagus to the muscular portion of the stomach, the gizzard (or ventriculus).

proximal. Nearest the trunk or midline; opposite of distal.

proximate chemical analysis. A series of standardized chemical analyses of organic materials to define their nutritional entities.

pteryla (pl. **pterylae**). A tract or area of skin from which the contour feathers grow.

race. See subspecies.

rachis. The vane-bearing shaft of a feather.

radius. The anterior, more slender bone of the forearm.

raptor. A raptorial bird; a bird of prey, e.g., hawks, eagles, owls.

recoveries. In the parlance of bird banders, refers to the identification of a banded bird that was killed or found dead. Direct recoveries are those of banded birds killed or found dead in the year of banding, indirect recoveries are those killed or found dead beyond the year of banding.

recrudesce (verb, **recrudescence**, noun). To renew activity, enlarge again; applied in this manuscript to the gonads.

rectrices (pl. of **rectrix**). Flight feathers of the tail, exclusive of the coverts.

remiges (pl. of **remex**). Flight feathers of the wing; attached to the ulna (secondaries) or manus (primaries); exclusive of the coverts.

returns. In the parlance of bird banders, refers to the identification of a live banded bird. Used by us with reference to birds that have survived from one year to the next, or beyond.

riparian. Frequenting, growing on, or living on the banks of streams or rivers.

scapulars. Feathers of the humeral feather tracts.

scutellate. Covered with scales (scutella).

secondary compounds. So-called "defensive" chemicals in plants, supposedly toxic, that deter feeding by herbivores.

secondary feather. One of the flight feathers (remiges) attached to the ulna.

sere. All the temporary plant communities or associations in a successional sequence. A *seral stage* is a floristically distinctive segment of a sere.

shrub-steppe. Plant associations dominated by a mix of shrubs and grasses, usually with few, or no, trees.

SMR (standard metabolic rate). Metabolism measured within the thermoneutral zone while an organism was at rest and in a postabsorptive state. Some authors equate this to **BMR**.

social. Living habitually together; living or associating in groups. Degree of sociality may vary seasonally and (or) by gender, age, and species. See also **antisocial**.

spermatogenesis. Sperm formation.

staminate cones. Male cones.

stand (re. to trees). Hammond (1991) says there is no settled definition of this term among foresters and other scientists. Paraphrasing his definition, we use "an easily recognizable unit of trees, in some way distinct from others around it".

sternum. The breastbone.

subspecies. Subspecies, often referred to as races, are cohorts of local populations that differ taxonomically from other geographic populations of the same species.

succession. A unidirectional change that can be detected in the proportion of species in a stand or for the complete replacement of one community by another.

superciliary. Pertaining to the eyebrow; supraorbital. Superciliary apteria are at times called combs.

syrinx (pl. **syringes**). The voice box of birds; located at the posterior end of the trachea, at the fork of the bronchi.

tarsometatarsus. The part of the bird's foot that bears the toes; a compound bone of birds, comprised of a small tarsal bone fused with four metatarsal bones.

territory. An area defended against intrusion by others of the same or different species. A territory may be part or all of a home range.

testis (pl. **testes**). Male sex glands (gonads) that produce spermatozoa.

tetraonines. The grouse and ptarmigan; species within the Subfamily Tetraoninae, Family Phasianidae.

thermograph. Instrument for making a continuous record of temperature.

thermoneutral zone. The range of temperatures in which metabolism is minimal.

tibiotarsus. The main bone of the lower leg (between the femur and the tarsometatarus); also called the tibia, but has tarsal elements fused to its distal end.

totalizer rain gauge. A device that collects precipitation over an extended period.

trachea. The windpipe.

turnover (annual, re. to populations). The amount of loss and replacement of members of a population from one year to the next; expressed as a percentage.

tympanum. 1. the eardrum; the middle ear cavity; 2. a sound-producing membrane in the syrinx; 3. used by some authors (inaccurately) to refer to the lateral cervical apteria of some male grouse.

ulna. The posterior, stouter bone of the forearm and to which the secondary feathers are attached.

uraemia. Retention in the blood of excessive amounts of nitrogenous wastes.

uropygial gland. A gland, located dorsally at the base of the tail (on the rump); its secretions are used in the care of epidermal structures, especially feathers; also referred to as the oil or preen gland.

vane. The flat, expanded part of a feather bordering the rachis (the shaft of the feather).

vector. A carrier, an agent transferring a parasite to a host, e.g., a biting fly.

ventriculus (gizzard). The muscular portion of the stomach.

vermiculated. Marked with fine wavy lines.

wolf tree. A conifer tree that has developed on open land; is short and stocky, with a wide and spreading crown.

yearling (also **ylg** or **Y**). A second-year grouse, sometimes referred to as a subadult; by our definition, beginning 1 January of its first winter to 31 December of its second winter. Unmarked yearlings cannot be separated from adults after attaining their definitive basic plumage, usually late September or October of their second autumn. See also **juvenile** and **adult**.

ylg (also **Y**). Abbreviation for yearling.

yolk. Inert, or non-formative, nutrient material in the ovum.

yolk sac. Extraembryonic membrane attached to the embryo of birds. Contains yolk, which serves as food for the developing embryo.

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